Disruption and disease: How does population management affect disease risk in wild bird populations?

Submitted by Beatrice Catherine Downing to the University of Exeter
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I certify that all material in this thesis which is not my own work has been identified and that no material has previously been submitted and approved for the award of a degree by this or any other University.

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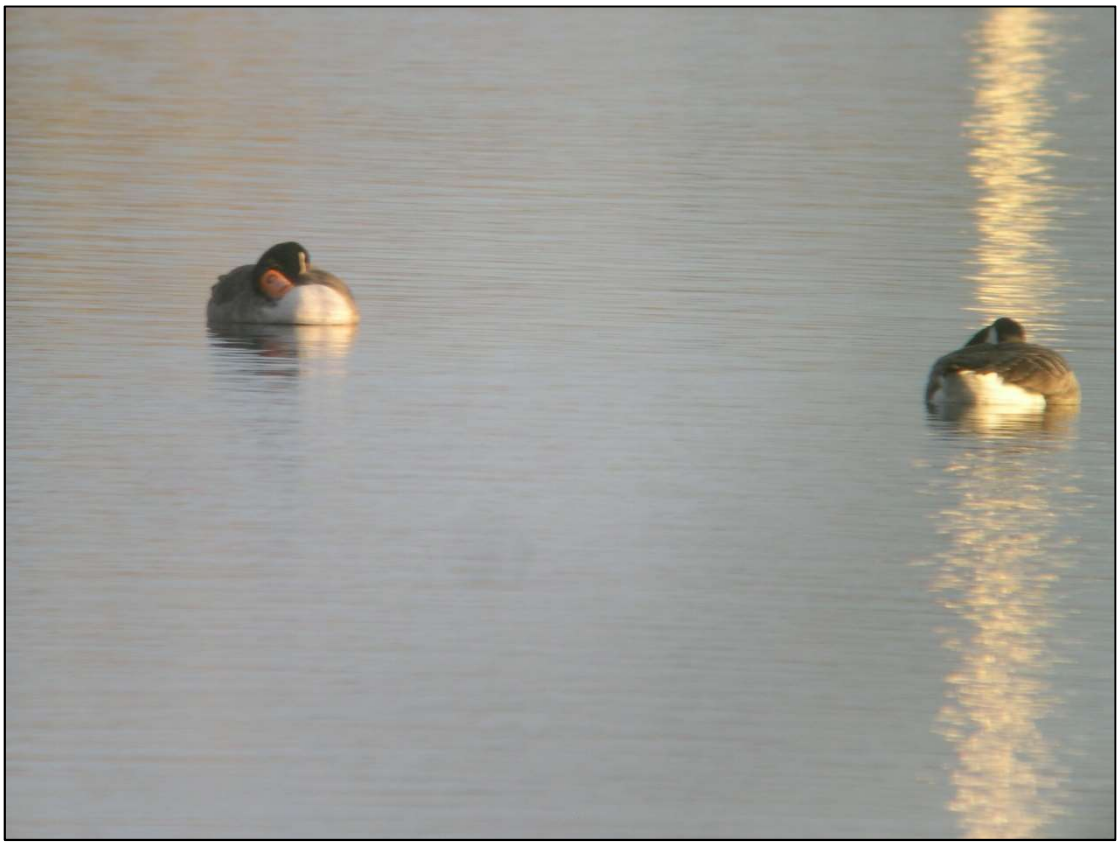

Abstract

Despite the ubiquity of wildlife management, from reintroductions and supplemental feeding to culling and habitat destruction, very little is known of the effects of management practices on species' social dynamics. Species' social structure has the potential to affect not only behaviour and evolution but also the transmission of information or disease. Understanding the effects of population management on social behaviour and organisation is a key step in understanding these species' ecology. This thesis examines the differences between individuals' roles in the social structure and what this means for the transmission of disease. It demonstrates how similarity in movement behaviour scales with increasing social circles, how seasonality in movement and seasonality in association rates covary as well as detailing post-cull behavioural changes. It finds that there is the potential for certain individuals (most likely non-breeding individuals) to transmit infection far and wide. It reveals the similarities in movement behaviour and body condition that birds share with their pair and social group. It emphasises the importance of autumn and winter movement in the transmission of infectious disease and it follows the short- and long-term changes in social structure and movement behaviour following a cull. Cull survivors were observed to retain a higher proportion of associations with their previous associates and moved less far in the year following the cull than in the year preceding it. This is the first application of social network analysis to quantify social structure before and after culling. The findings suggest that culling an infected population may facilitate rather than constrain the transmission of disease.

Acknowledgements

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Finally, thank you to Stephen, for everything.

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Author's declaration

Resightings data of the Cotswold birds were collected by BCD, with help from Stephen Downing, Matthew Silk, Mitch Weegman, Nick Royle and numerous members of the Cotswold birding community. The Thames dataset of resightings was collected and maintained by FERA.

All chapters in this thesis were written by BCD with thanks to Lucy Steward, Matthew Silk, Stephen Downing and my supervisors (Nick Royle, Stu Bearhop, Ruth Cromie and Dez Delahay) for their invaluable comments on earlier drafts of this work.

With these exceptions, I declare that the work contained in this thesis is my own and has not been submitted for any other degree or award.

Chapter 2
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1. General introduction

Animal species differ enormously in their social organisation: some only come together briefly to mate, some live in groups that change little from year to year, others live in highly fluid social systems where an individual's associates frequently change. Social structure has been observed to influence the transmission of information (Blonder and Dornhaus 2011; Kawamoto and Hatano 2014; Farine et al. 2015a; Clément et al. 2015; Firth et al. 2016), disease (Clay et al. 2009; Hamede et al. 2009; Leu et al. 2010b; Zohdy et al. 2012; Bull et al. 2012) and culture (Mann et al. 2012; Hobaiter et al. 2014). However, little is known about the resilience of social structure; most studies present snapshots of social structure within a season or over a year. Baseline temporal dynamics in social structure have been observed (Blonder and Dornhaus 2011; Jeanson 2012; Podgórski et al. 2014; Bierbach et al. 2014; Psorakis et al. 2015); however, the resilience of social structures to the removal of individuals has seldom been analysed. In a stochastic world, social species must adapt to the sudden loss of individuals and reorganise their social structure. Studies following this process in detail have been limited to captive populations (Jeanson 2012; Bierbach et al. 2014) and higher mammals with highly developed social systems (Goldenberg et al. 2016; Hobbs et al. 2017). This thesis is the first examination of how social structure and movement behaviour change following a partial cull in a free-living bird, the Canada goose (*Branta canadensis*).

In this thesis I describe the social structure and movement behaviour of free-living Canada geese before and after a partial cull. These studies reveal the impact of culling on goose social structure and the potential impact of culling on disease transmission dynamics. This thesis has three overarching objectives:

i) To describe the baseline social structure of a wild, free-living bird and the natural seasonal and individual variation in movement, social and physiological traits.

ii) To establish the extent of social disruption following a partial cull of the population.

iii) To evaluate the potential impact of changes in social behaviour and movement on the transmission of disease in this system.

Animals exist in social configurations of every shape and size: solitary species may come together to breed in discrete encounters (e.g. Tasmanian devil, *Sarcophilus harrisii*), group-living species form groups comprising a few individuals (e.g. wolves, *Canis lupus* (Borg et al. 2015)) or several thousand (e.g. honeybees (Naug 2008; Stroeymeyt et al. 2014)), with many species showing considerable seasonal variation in their aggregative behaviour (e.g. Brent geese, *Branta bernicla hrota*). Social structure affects contact rate: contact rates may be higher between mother and offspring (Stanton et al. 2011), between members of the same sex or age class (Streicker et al. 2012; Bhattacharyya and Ferrari 2017), or between individuals in the same area (Blonder and Dornhaus 2011; Stroeymeyt et al. 2014). This variation in contact rate is important because it may dramatically affect the transmission of disease (Drewe 2010; Leu et al. 2010b; Hamede et al. 2013). Certainly, variation in social behaviour means that individuals are exposed to different disease risks depending on social status: in Tasmanian devils, dominant individuals are thought to be at greater risk of acquiring Tasmanian devil facial tumour disease, via biting infected individuals (Hamede et al. 2013). Movement is important, with migrants seeming to amplify seasonal epizootics of avian influenza (Van Dijk et al. 2014). The most informative measure of contact rate is not necessarily the most basic: being the subject of aggressive contacts, rather than absolute contact rate, correlated with *Mycobacterium bovis* infection in meerkats (*Suricata suricatta)* (Drewe 2010), for example. Combining contact rate and infection status has the potential to reveal complex epidemiology (Bull et al. 2012).

Wild species are frequently managed to increase, decrease or redistribute populations. Species of conservation concern may be reintroduced to suitable areas (Fischer and Lindenmayer 2000; Godefroid et al. 2011), find themselves

with supplemented food (Chauvenet et al. 2012) or be protected by legislation against hunting (GOV.UK 2017) . Conversely, ‘pest’ species may be prevented from breeding, dissuaded or excluded from habitat and culled (Allan and Feare 1994; Wasserberg et al. 2009; Washburn and Seamans 2012). Despite the frequency of wildlife management, the impact of management strategies, including culling regimes, on social structure are not well understood. Culling may achieve its aim (Pandit et al. 2013); however, it would be as well to be cautious (Donnelly et al. 2006; Vicente et al. 2007; McDonald et al. 2008; Wasserberg et al. 2009; Beeton and McCallum 2011; Hallam and McCracken 2011; Abdou et al. 2016). A long-term study of badger (*Meles meles*) movement and social groups found management activity to be followed by badgers ranging further (Tuyttens et al. 2000) and a rise in disease prevalence (Woodroffe et al. 2006). Culling adult vampire bats (*Desmodus rotundus*) reduced the sizes of known colonies but did not reduce seroprevalence of the rabies virus, possibly because adults play a less important role in the transmission of disease than juveniles (Streicker et al. 2012). Indeed, periodic culling may lead to an increase in rabies virus seroprevalence in this system. Modelling the effect of culling on epidemic severity suggests that culls may increase not only disease prevalence but also the possibility of cross-species transmission (Choisy and Rohani 2006). These findings suggest that during culls to control disease transmission and outbreak size data must be gathered as to the effects on social structure and effectiveness in reducing disease.

The majority of emerging infectious diseases originate in wildlife (Jones et al. 2008) and those with high host plasticity are likely to be the source of the next human pandemic (Kreuder Johnson et al. 2015). Among emerging diseases, avian influenza viruses, which have in the past jumped from waterfowl to poultry and from poultry to mammals (Gavier-Widén et al. 2012), are an important concern. Avian influenza outbreaks can be enormously costly, both financially and in terms of loss of commercial flocks: the 2014-15 outbreak of avian influenza in 21 states of the United States of America has been estimated to have cost in excess of 950 million US dollars and resulted in the destruction of at least 50 million birds (David 2016). The *Anseridae’s* status as

asymptomatic carriers of several strains of avian influenza virus (Hulse-Post et al. 2005; Newman et al. 2009), their extensive use of shared waterbodies and their ability to travel great distances justifies ongoing research to establish their role in disease outbreaks (Munster et al. 2007).

This study calls for a species that is both highly social and subject to culling. Canada geese were introduced to the UK in the 17th century in ornamental wildfowl collections (Allan and Feare 1994). The habitat suited them and their numbers have soared since introduction. Their numbers have been estimated to exceed 88,000 individuals in Great Britain in 2000 (Austin et al. 2007). A more recent report placed their numbers at 56,000-63,000 breeding pairs, with a total population of between 346,000 and 356,000 individuals, in Europe (Kampe-Persson 2010). They are considered by Natural England a pest species and can be managed under licence to prevent damage to crops, foodstuffs and to prevent the spread of disease (Fox et al. 2000; Tsiodras et al. 2008; Jellison et al. 2009)). Management takes the form of the culling of adult birds (by shooting or lethal injection) or the destruction of eggs (by oiling or addling). Canada geese, like many *Branta* and *Anser* species, are highly social. Apart from the breeding season, during which pairs will vigorously defend territories, geese typically aggregate in flocks. Multi-species flocks comprising greylag (*Anser anser*), domestic (*Anser anser domesticus*) and barnacle (*Branta leucopsis*) geese have been observed (pers. obs) and hybrids are not unknown. *Branta* species show strong pair and familial bonds (Lindgren and Shapiro 1995), with the size of the family predicting dominance position within the flock (Poisbleau et al. 2006; Poisbleau et al. 2008).

The key role of social structure in the transmission of disease requires analytical techniques that are able to model this multi-directional structure explicitly. Social network analysis, which quantifies the frequency and distribution of interactions or associations made by every individual in a group, presents a way in which to define a population's social structure and the individual's role within it. Frequently used in epidemiological models of human disease (Fraser and Hawkins 1984; Meyers et al. 2005; Small et al. 2006; Vishkaie et al. 2014), social network analysis has revealed patterns in

sexually transmitted infections (Ashby and Gupta 2013), external parasites (Leu et al. 2010b; Fenner et al. 2011; Zohdy et al. 2012), SARS (Small et al. 2006), E. coli (Vanderwaal et al. 2013), brucellosis (Roy et al. 2011) and foot-and-mouth disease (Kao et al. 2007). Social network analysis has proven useful in modelling not only transmission but also the potential impacts of disease-control programs (Roy et al. 2011; Rushmore et al. 2014).

This thesis aims to establish the robustness of social networks to the removal of individuals and the effects on social behaviour and group stability of losing close connections. It also provides pre- and post-perturbation information on social and movement behaviour that will allow both disease managers and disease modellers to make more informed decisions. The thesis quantifies individual variation in movement, sociality and physiology. It then establishes baseline group-level variation in traits, before assessing seasonal variation in social behaviour at the population level. Finally, it evaluates the effects of culling on the movement and affiliative behaviour shown by this social species. It combines social network analysis and conventional multivariate analyses to establish baseline sociality and movement behaviour in Canada geese and the changes that follow a partial cull of the population.

Chapter two is a review of the literature and a basic primer to social network analysis techniques in the context of animal social systems.

In chapter three, the individual variation in movement behaviour, sociality and physiology is quantified. Individuals tend to be the basic unit in epidemiological models but the variation in contact rate, social network position and movement behaviour is seldom acknowledged. This chapter asks whether traits that could make individuals more important in the transmission of disease (e.g. contacting a large number of associates) are correlated. If greater sociality in this system is correlated with higher levels of movement, transmission may be amplified in highly social, highly mobile birds.

Chapter four focuses on the extent to which frequency of association correlates with similarity in movement behaviour and body condition. If close

associates are indistinguishable in their movement and variation exists at the level of the social group, it would be possible to model disease spread through social groups rather than individuals.

Chapter five reveals the seasonality within this system in terms of the movement of geese through the landscape and global structure of seasonal social networks. By combining social and movement networks and modelling epidemic spread in each season, this chapter suggests when transmission of contact-dependent and environmental pathogens may be fastest and extend furthest. This chapter employs not only the Cotswold Canada goose dataset used throughout this thesis but also a long-term dataset held by FERA of re-sightings of marked Canada geese in the Thames valley, UK. All epidemic spread data are taken from simulations of spread across observed networks.

Chapter six follows movement behaviour, affiliative behaviour and social network structure following a partial cull, which removed ~20% of the adult population at the study site. This is the first field study comparing social networks pre- and post-cull in a free-living bird.

Finally, in chapter seven (the general discussion) I discuss the findings and their implications for management of wild populations for disease control.

2. Animal social networks

Downing, B. C. and Royle, N. J. 2013. Animal Social Networks. eLS.

Social network analysis (SNA) is a powerful tool that allows researchers to understand and quantify the structure and dynamics of animal societies. It is particularly useful for studying the transmission of disease, information and culture in groups and within populations and the evolution of cooperation, but is likely to be applicable for almost any subject that involves animals interacting with one another. Social networks can be potentially constructed using any association or interaction as long as a significant proportion of the focal group/population is individually identifiable. Once networks are constructed summary metrics can be extracted and used to answer the questions of interest. Care must be taken to make sure that the metrics used are appropriate for the hypotheses under test. The continuous advances in technology mean that SNA is becoming more and more widespread and increasingly relevant to understanding animal societies.

Introduction

Social behaviour varies enormously not just across taxa but among individuals of the same species, or even the same population. Social network analysis (SNA) recognises that individuals often have distinct roles or positions within networks, and that these differences in how individuals interact with one another may have important biological consequences (Croft et al. 2008; Whitehead 2008).

The application of network theory is relatively new in ecology and behavioural studies. The tools that bioscientists use were developed by social scientists looking at the effects of environment on rehabilitation (Fraser and Hawkins 1984), epidemiologists investigating transmission of hepatitis B and HIV (Klovdahl et al. 1994) and network theorists keen to understand the control of resources in airport and collaboration networks (Opsahl et al. 2008).

SNA has since been used to quantify social structure in many different species, from cetaceans (Lusseau 2003) and primates (Henzi et al. 2009) to fish (Croft et al. 2005a), lizards (Godfrey et al. 2009), birds (Aplin et al. 2012) and insects (Pinter-Wollman et al. 2011), and to answer a wide range of questions, from understanding the transmission of information or disease through societies to the evolution of cooperation (Croft et al. 2005a). A network approach to the study of social behaviour puts the emphasis on how social interactions among individuals, not just the phenotypic characteristics of the individuals themselves, can shape variation in traits and affect important group-level, population-level and evolutionary processes (Fewell 2003; Royle et al. 2012).

What do we mean by social networks?

Social networks are most commonly constructed on the basis of one of two scenarios: (1) individuals share a defined area (e.g. a burrow, field, lake or perch) in an association or (2) individuals are observed to interact with one another. When individuals are judged to be associating as a result of being in the same group it is termed ‘gambit of the group’ (Franks et al. 2010) because assumptions are being made about group membership based on researcher-defined boundaries, and not based on interactions among animals (Whitehead and Dufault 1999). Data on social interactions (e.g. aggression, courtship, copulation or grooming) are often more difficult to gather but are likely to result in the construction of more informative networks. Interaction and association have very different meanings biologically and in network theory; therefore, ‘relationship’ will be used in this article when referring to both types of connection (consistent with Whitehead, 2008).

Nodes and edges: the bases of all networks

A network is formed of nodes connected by edges (Figure 2.1). The node (or ‘actor’) is the basic unit of analysis. In many studies, each node represents an individual, but this is not always the case. For example, in systems where

individuals form tightly knit groups and one is interested in the intergroup variation rather than the minimal intragroup variation, use of the entire group as the node avoids pseudoreplication and represents a more biologically relevant unit (Davis et al. 2007). Each edge (or ‘tie’) represents a relationship connecting two nodes. Where nodes represent individuals, the edge may be an interaction or an association and between nodes representing locations, the edge represents movement. When looking at movement and population dynamics, SNA using locations as nodes and movements as edges allows the identification of locations with particular properties, for example, areas with high rates of immigration (Kao et al. 2007).

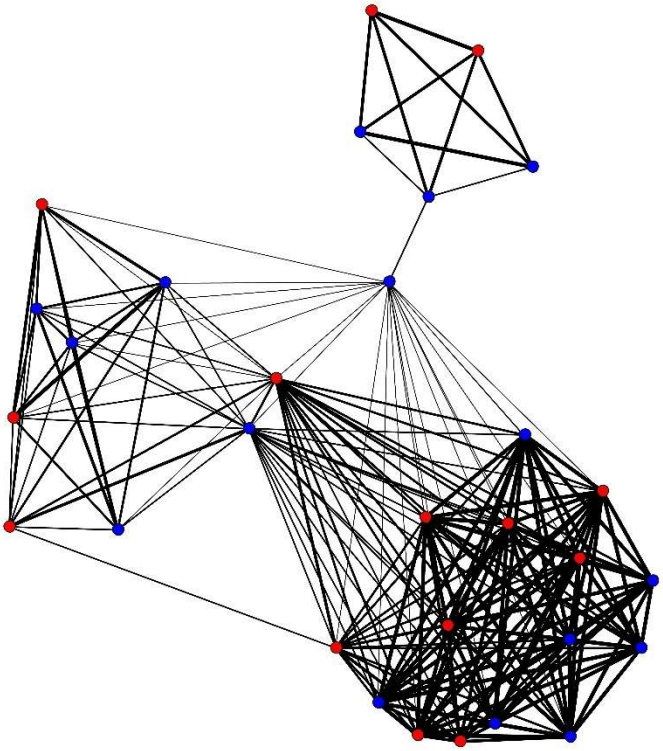


Figure 2.1. Toy sociogram (visualisation of network) showing nodes (filled circles) and edges (connecting lines) between three clusters of individuals within a group. Width of line is used to represent the strength of the edge, colour represents sex. The blue node connecting all three main clusters has the potential to be a ‘super-spreader’ of information or disease through the network as a whole due to its high betweenness.

Why take a networks approach to the study of animal social behaviour?

A great strength of SNA is its ability to account for multiple simultaneous interactions among individuals, which provides a more realistic picture of social relationships than traditional approaches. Conventional modelling of social behaviour as a series of dyadic interactions means that structure arising from triadic interactions or small clusters is invisible. As one accounts for more connections, one gains a truer picture of the nature of group dynamics and accounts for every relationship. This more accurately reflects the fact that the behaviour of individuals is both the cause and effect of their social environment (Royle et al. 2012). For example, the personality type of sticklebacks (*Gasterosteus aculeatus*) was found to affect who interacted with whom within shoals, so the composition of personality types within a group had a fundamental effect on the structure of stickleback social networks (Pike et al. 2008).

Building the Network

Edge choices

Any association or interaction can form the basis of a social network, and choosing the most appropriate measure for the question being posed is the most important decision involved in constructing a network (see (James et al. 2009) for a general review). Networks formed from associations are the most straightforward to build, as they require no detailed observation of behaviour, and all members of the group share the same level of association (the ‘gambit of the group’). In cryptic or shy species, this may be the only network possible. Rather than strict binary filtering, which removes information from the dataset much as using a rank order, networks can be weighted to make full use of the data. Weighting the edges by the number of times the relationship occurred (Whitehead 2008) is a way of retaining weak edges whilst assigning more importance to strong, frequently repeated relationships.

Interactions often contain directional information (directed networks). In certain interactions (e.g. fights and grooming), the direction of the interaction is clear and has obvious biological meaning. In other situations, for example, parental care of dependent young by great tits (*Parus major*), there is a clear directional interaction in the context of some behaviours, such as provisioning (parent/ provider and offspring/recipient) but not others (begging interactions among nestlings jostling for parental attention (Royle et al. 2012)).

As organisms display numerous different behaviours, it is possible to construct several networks from the same population using different measures of sociality or the same measure during different activity phases. Madden et al. (2009) observed that networks constructed from three different types of interaction (grooming, dominance and foraging competition) among meerkats differed markedly from one another. Once the appropriate edge measure has been chosen it is necessary to identify suitable nodes.

Node choice and marking

Building a social network requires being able to uniquely identify each individual or group that will be a node in the final network. Early studies relied entirely upon marks that were then resighted by observers. Intrinsic marks such as fin shape and condition are widely used for cetaceans (Lusseau et al. 2003) and extrinsic marks such as colour rings (Harrison et al. 2010a), paint or dye marks (Madden et al. 2009; Royle et al. 2012) or coloured tags (Otterstatter and Thomson 2007) for birds and mammals. Powder marking (Clay et al. 2009) and even uniquely coloured ticks (Zohdy et al. 2012) have allowed researchers to assign edges between individuals indicating physical contact in studies of disease transmission. These marks are cheap and often relatively easy to apply, with minimal effects on the behaviour and survival of most species, but rely upon observers to recapture data. In many wild species it is not possible to observe all meaningful interactions. Very well studied organisms such as the meerkat (*Suricata suricatta*) of the southern Kalahari

are watched for hours each day (Drewe et al. 2009) and also interact with one another underground out of sight.

Recent advances in technology have reduced the cost and size of tags, allowing marking of a remarkable number of taxa, from large vertebrates such as buffalo (Cross et al. 2004) to invertebrates such as ants (Jeanson 2012). Passive integrated transponder (PIT) tags (Jeanson 2012; Aplin et al. 2012), proximity loggers (Ji et al. 2005; Hamede et al. 2009; Marsh et al. 2011) and satellite tags can transmit information to base stations, removing the need for an observer in the field. PIT tags take their energy from the contacting base station, which records every time the unique tag is detected. Their small size and short detection distance (50–100 cm) means that these tags are most suited to small organisms such as ants (Jeanson 2012) and passerine birds (Aplin et al. 2012) and constructing networks based on social interactions around particular locations (e.g. foraging patches or nests). Loggers recognise and record signals from other loggers, so that meetings between tagged individuals of dispersed species are recorded and known; this has been used to determine contact rates and likely transmission of facial tumour disease in Tasmanian devils (*Sarcophilus harrisii* (Hamede et al. 2009)). Global positioning system and satellite tags record the location of the individual at a given time point, allowing the researcher to map movement of individuals; overlaying these paths then allows associating individuals to be identified (Leu et al. 2010a). However, even sophisticated tags are not without their problems: tags logging each close association have to be programmed to the association distance considered reasonable by the researcher and the margin of error on fixing a location, battery life, cost and reception distance (Drewe et al. 2012) all limit deployment.

It is important to emphasise that the final network structure will be affected not only by the choice of edges measured and nodes used but also by the method by which the data are collected; Perkins et al. (2009) found radio-tracking and capture-mark-recapture of the same population of yellow-necked mice (*Apodemus flavicollis*) yielded very different social networks.

Getting started

Once data have been collected they need to be converted into matrices that summarise the relationships (edges) among all nodes in the social group. This can be done by constructing edge lists (a list of the relationships among pairs of nodes, with a column for each of the two interacting/associating nodes and each interaction/association as a new row) that can be transformed into matrices (Figure 2.2) using software such as SocProg. Numerous packages, including SocProg, UCINET/Netdraw, Gephi and the tnet (Opsahl and Panzarasa 2009) and sna (Butts 2007) packages in R can be used to calculate network metrics and create sociograms from these matrices (Table 2.1). Sociograms allow the networks to be visualised for the identification of clusters and key nodes in the network. For further details on getting started see Whitehead (2008) and Croft et al. (2008), which are excellent, clearly written handbooks on social network analyses in animals.

Table 2.1. A selection of software used in social network analysis

Software	Use
SocProg	SocProg (Whitehead 2009) runs either within MatLab or as a standalone module and it transforms an edgelist into an association matrix. It can deliver association matrices constructed using half-weight, twice-weight, simple-ratio indexed and sum indices.
UCINET	A software package useful in calculating network metrics from association matrices (Borgatti et al. 1999). It contains NetDraw, which displays networks and calculates additional metrics for full and ego networks. It is available as a free trial version.
Gephi	Free open source software for Mac, Windows and Linux in which one can visualise data with sociograms and perform network analysis (Bastian et al. 2009). Datasets can be in the form of association matrices or edgelists.
R	tnet (Opsahl and Panzarasa 2009) and sna (Butts 2007) are packages calculating network metrics from association matrices that can then be plotted in igraph (Csardi and Tamas 2006). The statnet package covers exponential random graph modelling.

Assumptions and indices

Social network theory makes three key assumptions that need to be considered when applying social network analyses to real data. The first is that every individual in the flock, herd or shoal is represented as a node in the network. In some social systems, it is possible to unequivocally identify every individual and confirm that there is no immigration or emigration (e.g. in captive populations or networks of parents feeding dependent young (Royle et al. 2012)). In wild systems, the population is very rarely closed, and any unmarked, unidentifiable individuals will not be represented in the network. However, provided that the sample of marked individuals is not biased by marking only one class (e.g. adult males) or type (e.g. curious individuals

investigating traps and sick animals failing to evade capture) of animal, modelling indicates that most network metrics are resilient to only a small proportion of the population being marked provided weighted networks are used and there is frequent resampling of the marked individuals (Franks et al. 2010).

a)

Individual 1	AA	BB	CC	DD
AA	-	1	1	1
BB	1	-	0	0
CC	1	0	-	1
DD	1	0	1	-

Individual 2

c)

Donor	AA	BB	CC	DD
AA	-	1	0	2
BB	1	-	0	0
CC	4	5	-	3
DD	1	3	1	-

Recipient

b)

Individual 1	AA	BB	CC	DD
AA	1	0.50	0.37	0.83
BB	0.50	1	0.14	0.22
CC	0.37	0.14	1	0.64
DD	0.83	0.22	0.64	1

Individual 2

d)

Origin	Field 1	Field 2	Lake	River
Field 1	-	769	321	247
Field 2	453	-	687	342
Lake	168	1687	-	63
River	1036	985	54	-

Destination

Figure 2.2. Toy matrices showing data for SNA. (a) Binary symmetric matrix of an undirected relationship (e.g. association – nodes were either seen together (1) or not (0)); (b) half-weight symmetric matrix of association (AA and CC were seen together in 37% of observations); (c) asymmetric matrix of a directed behaviour (e.g. aggression) and (d) asymmetric matrix showing movement of individuals between sites.

The second assumption is that every edge is represented. Practical constraints often make it unlikely that this assumption can be met. For example, vegetation may obscure part of a group of foraging animals,

lowering the focal animal's number of associates that can be quantified. The third assumption is that individuals are equally detectable whether alone or in a group. As loud or brightly coloured animals may attract more attention when they aggregate, and large groups of animals are more obvious than small groups this assumption may also be violated.

All three assumptions are addressed by indices that correct for observer bias when building the association matrix from the edge list (Whitehead 2008). The most commonly used index is the half-weight index, which accounts for bias when marked individuals are more easily observed when apart than when together (i.e. if two groups are observed and the focal individual is equally likely to appear in either) and where not all of the associating or interacting animals have been observed. The twice-weight index is designed for use when two individuals are more likely to be recorded when together (e.g. when large groups are more obvious than small groups).

Metrics

One of the attractions of applying network theory is the ability to place an individual's behaviour or success in context by comparing it with that of other individuals in its group. These can be quantified using summary metrics. There are numerous different network metrics that can be used, depending upon the way in which the individual is to be compared with its group. The simplest metrics are count data: to how many others are the individuals connected (degree), and the number of connections the individual has with others in total (strength). These two metrics can distinguish between different social strategies – many weak connections or few strong connections for example – and are simple to calculate. Metrics such as clustering coeffcient and betweenness quantify the importance of the focal node in linking otherwise unconnected nodes (Table 2.2).

All the metrics mentioned above are suitable for both directed and undirected networks. Direction in network terms can only be calculated for interactions

(associations being undirected) but its use can reveal high levels of structure, such as the avoidance of diseased fish by healthy individuals (Croft et al. 2011a); b) and the unequal distribution of grooming in social mammals (Madden et al. 2011).

Not all metrics will be relevant to all hypotheses; to avoid data fishing (Sterne and Davey Smith 2001) it is important to understand the metrics relating to the question. Metrics that summarise how quickly things are transmitted through the network (i.e. path length and betweenness) will be relevant for understanding how disease or information spreads through social groups (Aplin et al. 2012). Metrics providing information on clustering and the centrality of individuals within networks (e.g. clustering coefficient and degree) will be especially informative when the research question is concerned with, for example, conflict/cooperation within groups (Royle et al. 2012). For more on the definition and use of network metrics, see the general review by Sih et al. (2009).

Table 2.2. Common metrics relating to nodes and networks

Level of analysis	Metric	Definition	Biological significance
Nodal	Degree	The number of other nodes to which the node is connected by an edge	Number of potential disease contacts, competitors or mates
	Strength	Degree weighted by the number of connections with each node, so that one can differentiate between weak and strong relationships	Proxy of duration of proximity or intimacy of contact
	Clustering coefficient	A measure of how many edges the nodes surrounding the focal node share with each other and varies between 0 (nodes around focal node have entirely dissimilar connections) and 1 (all nodes around focal node share the same connections)	A high clustering coefficient will mean that the focal node may have a lower probability of encountering a pathogen (because its contacts are mainly linked to each other) but a higher probability of being infected by the pathogen once it enters the cluster, as the pathogen will be presented by many sources, rather than one
	Betweenness	The number of shortest paths between two nodes on which the focal node lies	High betweenness indicates a central position within the network, which may leave the individual more

			vulnerable to disease, and the group less connected on the node's removal
Network	Path length	Mean path length is the average number of edges between each node in the network; minimum path length and maximum path length (diameter) quantify the network itself	Path length could be used to compare two networks created from the same population using different measures: for example, association and grooming frequency, to estimate how many steps it takes to get from one to the other
	Density	Number of existing edges divided by the number of possible edges	Dense networks will have shorter path lengths than sparse networks, resulting in a network with more alternative routes and the likelihood of faster and higher transmission

Autocorrelation, gambit of the group and spatial correlation

As networks are based on multiple simultaneous relation-ships among individuals, the data points in an association/ interaction matrix are not independent of each other. Different network metrics can be highly correlated with one another and some (e.g. degree) show autocorrelation; for example, if node A is connected to node B and C it has already influenced the degree scores of B and C. Consequently, no node can be removed without altering

the network metrics of other nodes. However, there are ways to deal with this non-independence. Statistical approaches such as general and generalised linear mixed models (GLMs and GLMMs) and exponential random graph models (ERGM) have both been suggested as methods of coping with heterogeneous network models with non-independent data points. ERGM express structural properties of networks (such as clustering coefficient); the probability or likelihood of these properties arising can then be calculated using methods such as Markov chain Monte Carlo models (Snijders et al. 2006). However, ERGM are more sensitive to incomplete datasets and therefore may not be the best choice for field data (Cross et al. 2012).

Gambit of the group is a widely used and informative approach, which is often applied when studying fission-fusion societies such as bottle-nosed dolphins (*Tursiops truncatus* (Lusseau et al. 2003), in which groups frequently come together, mix and separate again. However, caution must be applied; the researcher must decide whether all the individuals within the defined area are associating as a result of social affiliations rather than purely resource availability or territoriality. An individual may be reasonably considered to be interacting with all other members of the group if in a group of 6, but what if they are in a group of 60 or 600? Gambit of the group, when used in large groups, may overestimate degree (number of associates). On the other hand, if the question to be answered is ‘how many birds could a single bird infect at site A?’, the network may have to span more than the coexisting group members and include all individuals using the site of interest over a relevant time period. Two-mode networks (which plot two levels of information, for example, edges between individuals and between individuals and sites) can reveal shared associations and lagged association rates can account for how likely an association between two individuals is to reoccur within a set time period (i.e. after a time lag (Whitehead 2007)).

Considering permutations

The classic way of testing hypotheses using networks is to conduct permutation tests. These rearrange the observed matrix by either mixing up the edges between the nodes or swapping nodes between edges hundreds or thousands of times. The observed network is then compared with the thousands of randomly generated networks to decide how likely the observed network structures are to have occurred by chance. The Mantel test is a simple permutation test used to compare networks that is equivalent to tests examining the correlation between pairs of variables (e.g. Pearson's product-moment test). As the 'network' structure can arise from many processes, some of which may be completely extraneous (e.g. geography arising from site fidelity rather than social affliations), it is important to make sure that the comparison between observed and randomised networks is biologically meaningful. For example, it would make little sense to compare the observed network built from contacts within a cooperatively breeding long-tailed tit (*Aegithalos caudatus*) population, which exists in family groups, with a truly random network where every individual is assumed to be equally likely to interact with every other individual in the population. The two networks will always differ, but this will not reveal any novel information about the social structure. Social networks also have high levels of clustering that are not found in random networks (Newman and Park 2003). It is therefore often necessary to put in place certain priors before using permutation tests. For example, where there are strong social groups in a network, it may make sense to constrain randomised networks to have similar correlation coefficients, similar maximum degree or the same number of clusters as the observed network. For a review covering hypothesis testing using networks, see Croft et al. (2011).

Filtering down networks

Early papers used filtered binary networks, with edges the result of relationships that had been observed an arbitrary number of times to ascertain

their importance. Although this ensures that the relationship exists and is not the product of an observer error, there are often reasons for wanting to retain weak connections within the network (for a review, see James et al. (2009)). Transmission of disease, culture or information may arise from fleeting encounters; therefore, it is not possible to discount the importance of the transient relationship. Consequently, weighted networks should be used wherever possible (Whitehead 2008). Current options for analyses of weighted data are more restricted than those of binary networks but the new methods of analysis being developed will lift some of these constraints.

What questions can be addressed using SNA?

Sih et al. (2009) identified four key concepts associated with SNA that have the potential to generate new insights if applied to animal social biology:

i) Within-group differences among individuals in both their phenotypic characteristics and their social interactions can affect both individual and group outcomes (e.g. (Pike et al. 2008; Royle et al. 2012)).

ii) Indirect relationships matter (e.g. in transmission of information or disease).

iii) Individuals vary in their importance to the social network (e.g. ‘keystone’ individuals).

iv) Patterns of relationships in social networks can have carry-over effects across contexts (e.g. social network position in male–male competition may affect social position in mating networks).

These key components mean that novel insights can be gained from applying SNA approaches to tackle old problems on a wide range of issues, from mate choice and sexual selection to conflict and cooperation (Sih et al. 2009). SNA will also be useful in exploring new areas in social evolution, conservation biology and wildlife management. For example, SNA can be essential to our understanding of the transmission of information and disease (Christley et al. 2005). Clustering and heterogeneities within animal networks mean that simple density-dependence models cannot accurately predict disease

transmission (Vicente et al. 2007; Ferrari et al. 2011). The building of networks not only provides epidemiological information on disease transmission and the contact needed to become infected (Hamede et al. 2009) but also allows us to model the speed and penetration of disease transmission when particular individuals are infected (Keeling and Eames 2005; Porphyre et al. 2011). In studies of bovine tuberculosis in the European badger (*Meles meles*), plotting the ranges of social groups and SNA uncovered the effects of culling on disease transmission; though badgers were removed by culling, the perturbation caused breakdown of stable social clusters and an increase in badger movement, leading to increased opportunities for disease transmission (McDonald et al. 2008; Riordan et al. 2011). However, the applicability of SNA is widespread and is not limited to describing the social structure or understanding the transmission of the disease. We have only just begun to scratch the surface of possible applications of SNA to animal social behaviour, so the prospects for future work are exciting.

Future directions

SNA is ever more accessible to biologists as a direct result of advances in three areas: improvements in tracking technology to collect data, advances in statistical techniques by which to analyse datasets and increased awareness of the relevance and importance of taking a social network approach to understand the key issues in biology such as the link between individual behaviour and the phenomena that occur at higher levels of organisation such as the group or population (Croft et al. 2008).

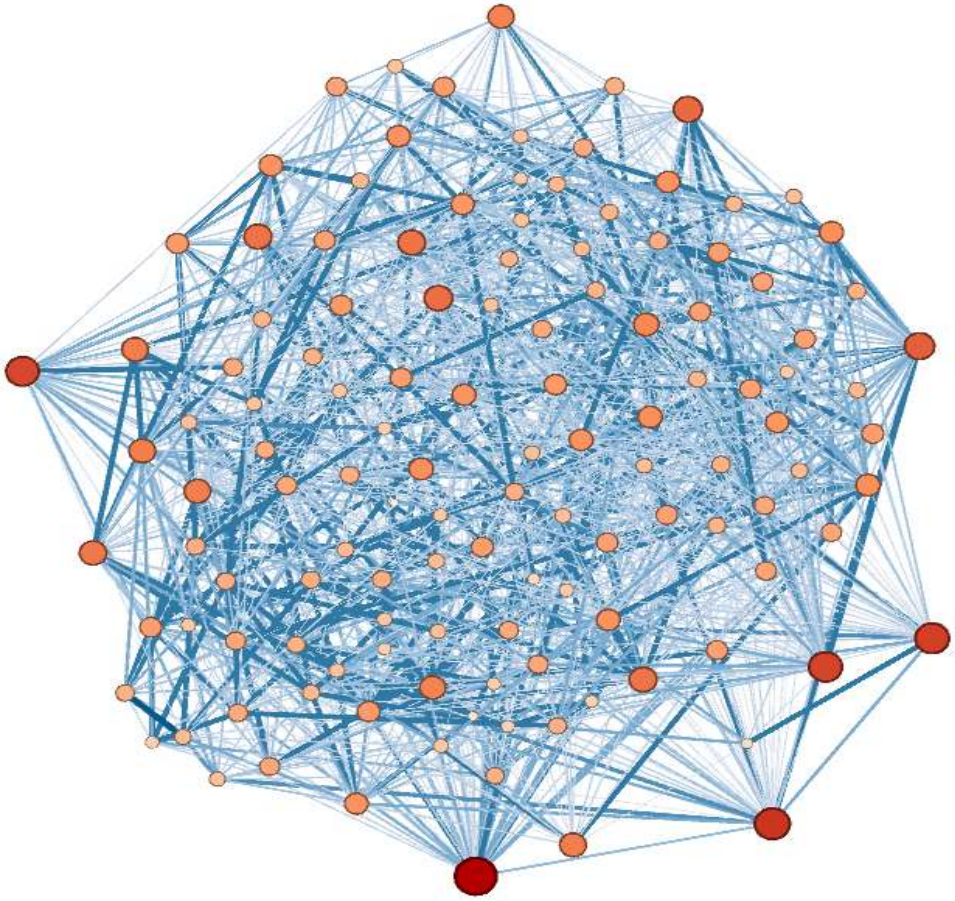
Improvements in tracking technology will mean that tagging and following animals to establish contact and interaction rates, as has been done for Tasmanian devils (Hamede et al. 2009), will become cheaper and possible in a wider range of species. Better battery life will allow tags to record more information and varying the frequency with which the record will yield datasets

that can be compared to assess how networks are affected by taking measurements at different scales.

Social networks do not exist in only two dimensions; there is a real need in biological systems for analyses of social networks to consider also time and geographic space. Lagged association rates (Whitehead 2007), stochastic actor-oriented modelling (Snijders et al. 2010) and hidden Markov models analyse changes in network structure at set time points. Recent advances allow continuous temporal change to be studied, by looking at how and when relationships within the network alter (Blonder and Dornhaus 2011). The most straightforward methods of acknowledging spatial information in social networks involve recognising where social clusters relate to spatial clusters (Pinter-Wollman et al. 2011), and in the future researchers will be able to assign clusters taking into account spatial information by using null models that have been built to reflect spatial clustering (Expert et al. 2011).

As the use of SNA in animal networks advances, the understanding of what constitutes a network will broaden. Researchers may move from using only parts of the sensory spectrum to building networks based upon aural and olfactory contact. It will be possible to move to studying finer scales of social dynamics (Haddadi et al. 2011). For example, adding information about the order or circumstances in which animals join groups to build directed association networks will improve our understanding of the rules that govern group fission-fusion. These rules may differ in birds, fish, mammals and insects, but using SNA it will be possible to disentangle the effects of preferred individuals, group size and disparity between the previous group and the new group in a powerful and systematic manner. The use of replicated networks is also a means by which we can gain an insight into how selection acts on groups and the (cooperating) individuals interacting with one another within those groups (Royle et al. 2012). This will improve one's understanding of the ecological and evolutionary importance of social networks (Fewell 2003) and determine how the behaviour of individuals can affect population-level processes (Croft et al. 2008).

3. Using social network, movement and body condition to predict individuals' ability to transmit disease.



3.1 Abstract

Individuals within a group may vary greatly in their social behaviour. Individuals that contact many others, from different social groups, may be more at risk of being exposed to or transmitting infection between social groups. Similarly, individuals that move across a wide geographic area risk being exposed to more pathogens than individuals that use a small number of sites. Both highly social and highly mobile individuals may act as 'superspreaders' within a population. Social network analysis, by quantifying contact rates between individuals, allows potential superspreaders to be identified and their social behaviour correlated to their physiology and movement. Social network metrics were correlated: birds that had many associates also had connections to more social groups. Social network position was also correlated with movement, in that birds with stronger connections had smaller home ranges. Non-breeding birds were found to have weaker connections to a larger number of associates, suggesting that they could infect more of the population if the infectious agent were easily transmissible. However, paired birds showed higher betweenness, which would suggest that they could infect more social groups. By targeted removal of non-breeding birds, disease managers may be able to remove the class of individual most likely to transmit infection widely, thus limiting disease spread. No metric of social network position correlated with body condition; however, the number of sites used by birds did predict condition. Thus, body condition could be used to identify highly mobile birds when seeking to control transmission of agents that can persist within the environment.

3.2 Introduction

Individuals vary in their movement and sociality, which can have important implications for the transmission dynamics of infectious diseases. The importance of determining the extent and effect of this individual variation has been widely recognised in the transmission of infectious disease, where some individuals may play a more important role (Lloyd-Smith et al. 2005; Rushmore et al. 2013). The effects on disease dynamics of individual variation in gregariousness, home range size and movement patterns have been explored for a wide variety of species (Otterstatter and Thomson 2007; Hamede et al. 2009; Bull et al. 2012; Rushmore et al. 2013). However, few studies have focused on species that live in large groups for most of the year, whilst also moving great distances. Hence, little is known about how social interactions may affect transmission dynamics in species where a single individual has the potential to infect many others at a large spatial scale.

In any population, certain classes of individuals may be of greater interest to disease managers. For example, individuals that contact a large number of others (Rushmore et al. 2013; Rushmore et al. 2014) and that contact several distinct social groups frequently (Christley et al. 2005; Leu et al. 2010b)) may have the potential to infect an unusually large number of naïve individuals (Lloyd-Smith et al. 2005). These potential superspreaders have been identified in studies of disease transmission in Tasmanian devils (*Sarcophilus harrisii)* (Porphyre et al. 2008). In badgers *(Meles meles),* infected individuals were found to occupy social positions that facilitated spread amongst social groups (Weber et al 2013). In networks of cattle movements, certain locations were identified to be important in the wide transmission of foot-and-mouth disease (Kao et al. 2007). An effective superspreader (in terms of ability to accelerate the transmission of a pathogen through a population) would contact a high number of different individuals in such a way as to facilitate transmission. For group-living species, this would involve contacts amongst members of several distinct social groups that would otherwise be more socially isolated (Loveridge and Macdonald 2001; Russell et al. 2006; Craft et al. 2011). High mobility (Craft et al. 2011), for example using numerous

resting or foraging sites over a wide area, would also increase the individual's exposure to infection and the area of potential environmental contamination (Craft et al. 2011; Weber et al. 2012).

Social network analysis is changing the way we view disease transmission by revealing unseen transmission paths in many species, including humans (Fournet and Barrat 2014; Vishkaie et al. 2014), primates (Zohdy et al. 2012), lizards (Fenner et al. 2011; Bull et al. 2012), and particularly those that are traditionally difficult to study (Hamede et al. 2009). Modelling group- or population-level processes, such as the transmission of disease or information, without considering the effects of individual variation in sociality creates models which may not reflect reality (Lusseau and Newman 2004). The spread of directly transmitted pathogens may be limited in species that are spatially or socially constrained in their contact with others (Baracchi and Cini 2014), which may be linked to territoriality (Delahay et al. 2000; Drewe et al. 2009) or solitary lifestyles (Ji et al. 2005; Böhm et al. 2008; Haddadi et al. 2011). Social network analysis allows us to move beyond simple dyadic models, or models in which homogeneous groups are composed of blank, interchangeable units, to realistic reflections of observed populations (Sih et al. 2009). For a truly gregarious species, social structure is likely to have a profound impact on disease dynamics and social network analysis is a powerful tool for understanding this structure.

Characteristics such as breeding status, rank and condition, factors that are themselves interrelated, are likely to influence movement and sociality, and thus social network position. For example, in dark-bellied brent geese (*Branta bernicla bernicla)* families were found to be dominant over pairs, which were dominant over single birds (Poisbleau et al. 2006). To be subordinate in this system can mean exclusion from preferred habitat (Alatalo and Moreno 1987; Black et al. 1992), which is likely to result in increased movement (Gyimesi et al. 2010), utilisation of habitat with a higher risk of predation (Schneider 1984; Hegner 1985) and reduced body condition (Poisbleau et al. 2006). Subordinate geese may also experience an increase in aggression, resulting in a need for greater conspecific vigilance (Black et al. 1992) and reduced

time foraging or resting. Therefore, it is likely that body condition, resulting as it does from the individual's ability to access resources whilst reducing unnecessary movement, is linked to dominance, with dominant birds that can retain access to the best resources being in better condition. In order to assess whether there is an energy cost to the movement levels observed in this system, body condition can be used to identify whether there is a correlation between condition and movement levels. If birds in poorer condition are more likely to move and/or move long distances, then management interventions targeting subordinate birds (such as those appearing in non-breeding flocks during the breeding season) may be more likely to reduce the risks of disease spread than untargeted management approaches.

Individuals may show variation not only in the distance travelled, area covered or number of sites used but also in the predictability of those movements (Phillips et al. 2003). Many species that move long distances use the same staging areas year on year, showing high levels of site fidelity as a species but with considerable individual variation (Hestbeck et al. 1991; Balkcom 2010). Site fidelity in migratory birds can be higher in successful breeders (e.g. greylag geese, *Anser anser* (Kruckenberg and Borbach-Jaene 2004)). Fidelity to particular sites is heritable, with offspring returning to their parents' previous staging sites (Greenland white-fronted geese, *Anser albifrons flavirostris* (Fox et al. 2002)). Though in resident Canada geese (*Branta canadensis)* migration has been suppressed, which is thought to be partially the result of introduced birds not possessing any inherited knowledge of migration routes (Sutherland 1998), they are still likely to show strong site fidelity and have demonstrated flexibility in their movement behaviour. Individual variation in site fidelity will influence the likelihood of pathogen exposure and transmission and therefore may be an important consideration for disease managers.

Two sources of individual variation that pertain to disease transmission in a wild population will be investigated in the present study. The first is the individual variation in network position: i.e. how heterogeneous is this population in terms of their network metrics and thus their sociality. Are

individuals' network positions undifferentiated, with largely identical numbers of associates or connections to different social groups? Second, is the individual variation in movement propensity and home range; particularly the movement behaviour shown by individuals that contact several different social groups. These individuals with the network position of potential superspreaders could have an additional effect in transmitting disease if they also range further than individuals in other network positions.

Wild Canada geese present a suitable study system in which to explore the potential impact of social structure on disease transmission. They are an extremely social species that may travel long distances (Wege and Raveling 1983), gathers in large numbers (Forbes 1993), forms mixed flocks with other Anseriformes (Fabricius et al. 1974) and commonly frequents sites used by humans and domestic animals (Forbes 1993). Canada geese are also known to be reservoirs and vectors of several pathogens including *Campylobacter jejuni* (Pacha et al. 1988)*, Escherichia coli* (Benskin et al. 2009; Garmyn et al. 2011)*, Cryptosporidium spp* (Graczyk et al. 1998; Zhou et al. 2004)*,* avian paramyxoviruses (Kruckenberg et al. 2011), duck plague (Bonner et al. 2004) and the important human pathogen *Helicobacter pylori* (Waldenström et al. 2003). For this reason alone their frequent presence on amenity grassland and waterbodies can be of concern. In addition 50 geese can produce 2.5 tonnes of waste per year, with the associated risks of pathogen persistence in their faecal deposits (Feare et al. 1999).

The impact of social structure on disease transmission is particularly relevant when considering Canada geese, as in the UK this species frequently occurs alongside humans in large numbers, and is periodically the subject of management interventions. Management takes many forms: culling of flocks, egg oiling or destruction, barriers and deterrents (Smith et al. 1999). Culling and destruction of eggs (whether through addling, pricking or oiling) may have the potential to alter social structure in different ways, with culling operations potentially removing entire social groups (possibly with certain behavioural attributes. Egg destruction artificially forces nest failure, which has been

shown in many species to increase the rate of divorce (Dubois and Cézilly 2002) and would alter the dominance ranking of pairs.

In order to estimate the potential impact of social structure on transmission dynamics in this species, this study quantifies the variation in sociality within the network to establish whether there are individuals that contact high numbers of individuals from different social groups. Potentially risky behaviours for pathogen transmission (e.g. contacting many individuals or linking distinct groups) may be evenly spread across the population. However, the goose social system and potential for correlation between social network metrics suggests that certain individuals may be both highly gregarious and contact different groups, traits that become multiplicative when displayed by the same individual. Birds that are highly gregarious and contact high numbers of conspecifics from several different groups, thus becoming potential superspreaders, are likely to do so by visiting many sites over a wide area, setting up a positive correlation between sociality and movement behaviour. Birds that are more socially stable (those with several strong connections and few weak connections) would be expected to be more faithful to their moult site. This would be due to their strong social connections meaning both dominance at the site and because they have displayed repeatable preferences in their associations. Birds in poorer condition, of lower body weight, and unpaired birds may be more likely to be displaced from sites and form fleeting alliances with casual associates (Sandell and Smith 1991; Farine et al. 2012). By combining movement and social network information, potential superspreaders can be identified, and management interventions may be tailored to target them.

3.3 Methods

Study system

The study area (Ordnance Survey grid reference SU 0796) is an area of working and restored gravel pits covering 85 km^2 within the Cotswold Water Park (CWP), near Cricklade, Wiltshire, UK (OS grid reference SU 09857 93574). The 140 waterbodies of the CWP are largely privately owned and managed, primarily for water-sports and angling, but the Cotswold Water Park Trust oversees the area (which includes land in Wiltshire, Gloucestershire and Oxfordshire) and has the role of recording and advising on biodiversity and wildfowl management. The lakes are surrounded by farmland, nature reserves, holiday accommodation and small settlements. Canada geese are resident at this site all year round with a wintering population in excess of 600 (Holt et al. 2015). The combination of numerous water bodies bordered by amenity grassland and arable fields provides much suitable habitat for this species and the main methods of population control are planned management by shooting and egg oiling. The study area was a 6km strip running 23km east-west across the water park.

UK-resident Canada geese form flocks consisting of 3-400+ birds depending on season and region. During the breeding season (March-June), breeding pairs split off and defend territories, whilst non-breeding birds remain in flocks. Canada geese moult their flight feathers, annually timed to follow breeding. During the moult, breeding pairs, offspring and non-breeders congregate together in moulting flocks. This flightless period extends from June into July, when entire flocks can be caught. Birds are known to live for 25-30 years, though the average lifespan is thought to be closer to 15 (Patuxent Wildlife Research Center 2011).

In order to mark individual geese, five moult sites distributed across the park, (with a maximum geodesic distance between sites of 16.93 km, and a minimum of 1.61 km) were identified as catch sites (Figure 3.1).

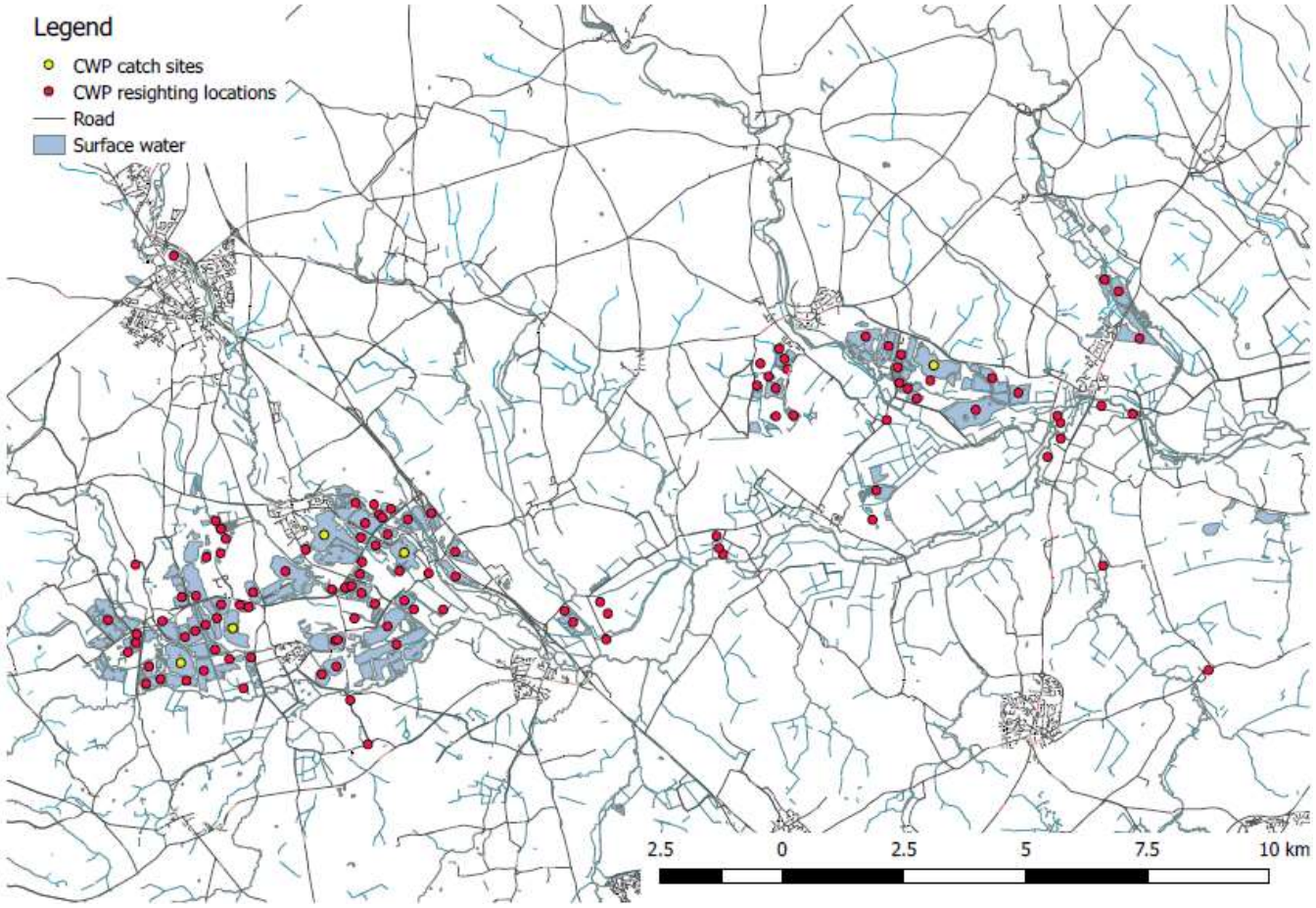


Figure 3.1. 2012 catch sites at the Cotswold Water Park (CWP).

On 3rd and 4th July 2012 geese were rounded up on the water by an experienced team of kayakers and driven on land and into a screened pen. Individual birds were then taken from the pen and fitted with highly visible neck collars bearing unique codes and metal British Trust for Ornithology (BTO) leg rings in accordance with local ringing practices. Neck collars (dimensions: inner diameter = 42mm, height = 65mm; Interrex, Łódź, Poland) were formed of black plastic overlaid with orange, so that the two-letter codes appeared as black text on an orange background. In total, 174 geese were fitted with metal BTO leg rings, of which 153 adult birds were fitted with collars.

Construction of the networks

Collar codes of marked individuals were recorded in the field by an observer with binoculars and a telescope. Group membership, location, flock size, time and date were also recorded. Resightings took place on 146 days between July 2012 and June 2013, resighting in every month of the year and from dawn until dusk. Birds in a flock present at the same site at the same time were judged to be associating, and the code of each bird was recorded as a member of that group. This method of network construction, termed ‘gambit of the group’ (Whitehead and Dufault 1999; Franks et al. 2010) assumes that, over time, individuals will be observed most frequently with those with whom they have a biologically meaningful relationship. The extent of flock membership was determined by a chain rule based on local geography and the distances between birds – birds were considered to be within a flock if they were in visual contact, were not separated by barriers such as hedges or by distances four times greater than the mean inter-individual distance (measured in goose body-lengths to allow accurate calculation of distances at distance). On water bodies, all individuals present on the lake were termed associating. In the field, groups of geese tended to stay away from field margins or boundaries and self-organised into cohesive flocks. All fission-fusion events were recorded, and small groups of individuals that arrived or departed separately from the main flock were recorded both as part of the

large flock and as a subunit in separate events. A matrix of these co-occurrences was then used to calculate an index measuring strength of association between birds. The half-weight index is commonly used in social network analysis for the construction of social networks where nodes are more likely to be observed when not associated, or when not all individuals can be identified (Whitehead 2008). The half-weight index assigns each pair of individuals an association strength based on the number of times they are seen together (x) versus separately in different periods (y_A+y_B) or separately in the same period (y_{AB}).

$$\text{Half-weight index} = x/(x+y_{AB}+1/2*(y_A+y_B))$$

Calculation of social network metrics

Association matrices, networks and metrics were calculated based on the full year of resightings (June 2012-June 2013). These whole-year networks ignore seasonal variation and look for overall patterns of association and network position across the year. Degree, strength and betweenness were calculated in R (version 3.2.0, package ‘sna’ (Butts 2007)) for birds with 10 or more resightings (n=145), Figure 3.2.

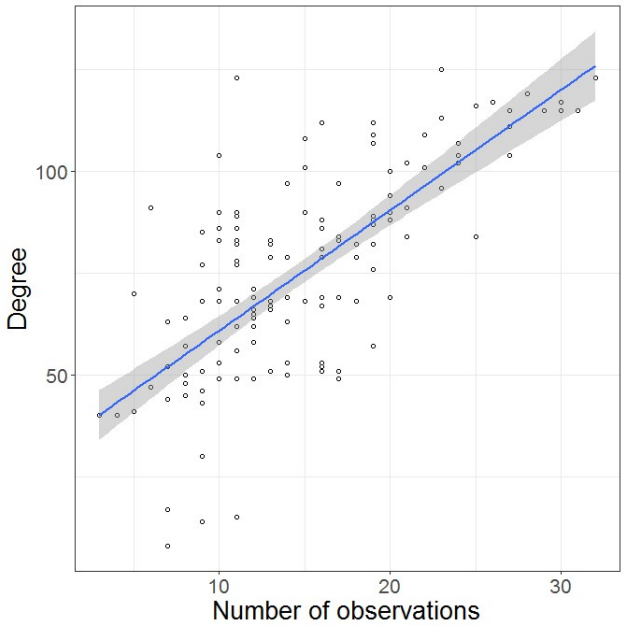


Figure 3.2. The relationship between degree and resighting rate for all Cotswold birds.

Degree is the number of other individuals with which the focal individual associated. Strength is degree weighted by the number of associations and can increase in two ways: by increasing the number of associates, or by associating more frequently with those associates (Whitehead 2008). Here, strength was calculated using the half-weight index, which minimises bias when not all associates are recorded (Whitehead 2008). Betweenness (also known as betweenness centrality) calculates the shortest paths between every pair of individuals in the network; each individual's betweenness then reflects the number of shortest paths in which they feature. Betweenness reflects how important each individual is in connecting clusters (subgroups within a population) that would otherwise be discrete. Degree and strength were corrected for number of observations by regression calibration: recalculation from residuals of an ordinary least squares regression (Rosner et al. 2006). Spearman's rank analyses were used to identify correlations between degree (corrected for observation level), strength (corrected for observation level) and betweenness, taking into account the non-independence of data (Farine 2015).When calculating metric matrices, the degree matrix was a binary association matrix with a 1 representing the presence of an association between bird i and bird j, and 0 its absence. The

strength matrix gave the half-weight indexed strengths between each pair of birds. The betweenness matrix gave the difference (positive or negative) between the betweenness scores of each pair of birds.

Morphometrics and assignment of paired/breeding status

Each captured bird was weighed in a hessian sack suspended from a zeroed spring scale (Pesola©) measuring mass to the nearest 10g, and skull (head and beak) and tarsus length (being considered to be the most accessible and repeatable skeletal measurements (Black et al. 2014)) were measured with callipers to the nearest millimetre. Sex was established for 115 birds by cloacal examination performed by experienced staff (Hanson 1962). This entailed eversion of the cloaca to detect the presence or absence of the penis and is estimated to carry an error rate approaching 15%, which is biased towards the miscategorisation of males as females (Cooch et al. 1996). Scaled mass index, a proxy of body condition, based on skull length and mass, was calculated after Peig and Green (Peig and Green 2009). In this calculation mass, M_i, length, L_i and an arbitrary value of L, L_0 are scaled by b_{SMA}, the slope of the standard major axis regression of the biometric L to give ˆMi, which is the predicted body mass for individual *i* when the linear body measure is standardised to L_0. This scales the mass of all individuals to that expected for a given body size and is, therefore, dependent on the sample of the population measured. In order to calculate the change in scaled mass index between years, all measurements from both years were combined into a single dataset, the slope of the relationship and the standard major axis were recalculated and birds were indexed according to their position in this dataset in both years.

$$\text{scaled mass index: } \hat{M}_i = M_i \left[\frac{L_0}{L_i}\right]^{b_{SMA}}$$

Breeding pair status was assigned to adults that were observed to be defending territory (e.g. nest sites) or offspring in February-August in the year of interest. Breeding success was assigned to adults guarding downy goslings

or juvenile geese, either alone or with one other adult, in March-July in the year of interest.

Calculation of movement behaviour

Movement behaviour was assessed in two ways. Firstly, the number of sites used by each bird over the year was calculated, which was useful at a small scale for distinguishing between birds that frequently moved between geographically close but separate lakes. Sites were defined as single lakes or fields, within which there were no barriers (vegetation, fences) that would prevent birds from being in visual contact with others at the site, or that would prevent free movement by the birds walking across the site. This value was normalised by taking the residuals from a regression of number of sites vs number of observations and adding them to the mean, resulting in a corrected value giving the number of sites used for the known number of observations. Secondly, each bird's core 20% home range was calculated to give a better understanding of the area used by each bird over the year. Home ranges were calculated by assigning latitude and longitude to each observation of every bird. These points were then used to calculate utilisation distribution kernel estimations (Worton 1989) in R (version 3.2.0, package adehabitat (Calenge 2006)), which provides not only the total home range but also the 20% of the range that is used most frequently. In line with previous research (Baracchi and Cini 2014), utilisation distribution home range kernels at the 50% and 95% levels were also calculated, but variation at these levels was skewed by the presence of outliers, which was not the case at the 20% utilisation distribution level. Geographic region, a three-level categorical variable of 'east', 'west', 'central', was included in analyses of movement to capture regional variation in movement that might be due to local farming patterns, landscape features and crop availability.

Statistical analysis

Correlational analysis

Correlation tests of metric matrices were performed in R (version 3.2.1), using package Hmisc (Alzola and Harrell Jr 2006), to calculate Spearman's rho. Degree and betweenness matrices were compared to a half-weight indexed strength matrix to assess whether a trade-off existed between the number of associations an individual formed, and the strength and social reach of those relationships (Valente et al. 2008). High-degree birds are likely to be more important than low-degree birds in the transmission of disease, but this effect is amplified if high degree correlates with high betweenness as predicted, meaning that these birds are also contacting many social groups.

Matrix permutation analysis

The non-independence of social network data necessitates permutation methods for examining how well degree, strength and betweenness explain the biological variation in scaled mass index (a proxy of body condition), number of sites used and home range (Farine and Whitehead 2015). Multiple regression quadratic assignment procedure (MRQAP) allows matrices of attributes (e.g. matrices in which the value for column *i,* row *j* will appear as, for categorical variables, 0 if individuals *i* and *j* are dissimilar, and 1 if they are similar; for continuous variables, the difference between individual *i* and individual *j*) to be regressed on association matrices (matrices giving the number of times individual *i* has been seen with individual *j*) to understand which character attributes (here breeding status, body condition, sex, home range size or number of sites used) best explain the association matrix retrieved from observational data. Double semi-partialling MRQAP (MRQAP-DSP) is a technique that looks for correlations between matrix X and matrix Y while controlling for matrix Z (Dekker et al. 2007). In MRQAP-DSP, collinearity between variables is accounted for by partialling the effect of the additional variables (Z) out of X, permuting the residuals and regressing Y onto both

these residuals and Z (Dekker et al. 2007). For example, in the first model run, degree (matrix X) was used to predict variation in number of sites used (response variable, matrix Y), while controlling for geographic region (matrix Z).

Three sets of MRQAP-DSP models were run in R (version 3.2.0, package asnipe (Farine and Whitehead 2015)) to explore the distribution of network metrics and biological variables by regressing three matrices (based on the three social network metrics: degree, strength and betweenness) onto that of the biological variable.

i) Network position and movement: nine models exploring how well matrices of degree, betweenness and strength explain three measures of movement propensity for each of the three geographic regions. The three movement matrices were a normalised number of sites used (a matrix of positive/negative differences in number of sites used), the 20% home range size (a matrix of absolute difference between the area of each pair of birds' home ranges) and site fidelity (a matrix of moult site fidelity similarity, in which the value in row i, column j was 1 if both bird i and bird j showed the same fidelity behaviour and 0 if not).
ii) Network position and paired/breeding status: two models exploring how well matrices of degree, betweenness and strength predict breeding and paired status. Paired and breeding status similarity matrices were calculated as for the site fidelity matrix.
iii) Betweenness and body condition: a single model was run correlating a matrix of betweenness with matrices of 2012 scaled mass index and the change in scaled mass index relative to the population between 2012 and 2013.

Skewness of strength distributions was calculated in R (version 3.2.0, package 'e1071' (Joanes and Gill 1998)).

Model selection by AICc

In order to explore the relationship between movement and body condition and mass, beyond variation that could be due to social factors within the population, two sets of candidate models were developed: firstly, to predict movement behaviour (short-range movement propensity and 20% utilisation distribution of the home range) from initial (2012) body condition and mass; secondly, to assess the impact of movement behaviour on the change in body condition (∆scaled mass index) seen between years (2012-2013).

In predicting movement behaviour from initial body condition and mass, two hypotheses were posed: i) do birds in poorer condition (using scaled mass index values in 2012) move more than those in better condition ; ii) do birds that weigh less (regardless of condition) move more. In all, 52 candidate models were developed to assess the correlation between body condition and mass in 2012, and subsequent movement levels (number of sites used across the year corrected by number of observations) and the area of the core 20% of home range, calculated from the utilisation distribution kernel (Worton 1989).

In predicting a change in scaled mass index as a result of high levels of movement, the hypothesis was that birds that lose condition (a reduction in scaled mass index relative to the population between years) move more (Table 3.1). A further 27 candidate models were used to assess the impact of movement levels and 20% home range area on the change in body condition (∆scaled mass index, Table 3.1). Sex was included as a fixed factor only in models containing mass. Pairs were assigned a grouping factor rather than being treated by the models as completely independent; all paired or breeding birds where the mate was unmarked were assigned the same value for this factor.

Linear mixed effects models were constructed in R (version 3.2.0, package lme4 (Bates et al. 2015)) and then ranked by the corrected Akaike Information

Criterion (AICc) using AICctab (package ‘bbmle’ (Bolker and Team 2014)). Models within two AICc units of the top model were then averaged using model.avg (package ‘ MuMIn’ (Barton 2015)). Model averaging takes the candidate model set and runs all models on the same dataset. Coefficients of each model were then averaged in the final summary, each model was given an AICc value to describe the fit of the model to the data given the number of parameters, and variables were assigned importance depending on how well they explained the data, with variables ascribed a high amount of importance ranked the most influential within the models (Harrison et al. 2013). Six candidate models were averaged to assess the correlation between body condition and mass in 2012 and subsequent movement propensity, and five to assess their correlation with range size. Two candidate models within three AICc units were averaged in assessing correlation between change in body condition and each measurement of movement level.

Ethics Statement

All work was carried out in the UK in accordance with University of Exeter and AHVLA Ethics guidelines and under Natural England and British Trust for Ornithology licences. All field procedures were approved by the University of Exeter Ethics and Health and Safety Committees. All work was carried out with land owners' permission.

Table 3.1. Terms used in candidate models.

	Terms	Type		
Model set 1	Number of sites used	Response	Fixed	Continuous
	20% home range	Response	Fixed	Continuous
	Body condition 2012	Explanatory	Fixed	Continuous
	Mass 2012	Explanatory	Fixed	Continuous
	Paired status 2012	Explanatory	Fixed	Categorical
	Paired status 2013	Explanatory	Fixed	Categorical
	Breeding status 2012	Explanatory	Fixed	Categorical
	Breeding status 2013	Explanatory	Fixed	Categorical
	Sex	-	Fixed	Categorical
	Pair ID	-	Random	Categorical
	Moult site	-	Random	Categorical
	Geographic region	-	Random	Categorical
Model set 2	Δ body condition	Response	Fixed	Continuous
	Number of sites used	Explanatory	Fixed	Continuous
	20% home range	Explanatory	Fixed	Continuous
	Paired status 2012	Explanatory	Fixed	Categorical
	Paired status 2013	Explanatory	Fixed	Categorical
	Breeding status 2012	Explanatory	Fixed	Categorical
	Breeding status 2013	Explanatory	Fixed	Categorical
	Pair ID	-	Random	Categorical
	Moult site	-	Random	Categorical
	Geographic region	-	Random	Categorical

3.4 Results

Resighting rate

All marked birds (n=153) were resighted over 3212 resightings in 394 events. Following removal of eight birds with fewer than ten resightings, the mean resighting rate was 21.74, range 10-44, n=145. For the 353 resightings for which flock size was known, a mean of 48% of birds within the flock were marked.

Correlational analysis

Network metrics were found to be highly correlated, with highly gregarious birds (those with high degree) also contacting many birds frequently (high strength) across several separate social groups (high betweenness) (Spearman's rho 0.778, $p<0.001$). Degree and strength were also significantly correlated (Spearman's rho 0.404, $p<0.001$) but strength and betweenness were not correlated (Spearman's rho 0.027).

Matrix permutation analysis

Flock membership was important in the relationship between home range size and degree, with high degree birds from the eastern region ranging further than their regional con-specifics (though not further than birds with the same degree from the wider population) (Figure 3.3). In the central and western regions of the study area, high degree birds had smaller home ranges than lower degree birds.

However, birds with high strength associations had smaller ranges than those with lower association strengths (Table 3.2). Flock membership was important in this relationship, with a negative correlation between home range size and strength for all birds, but stronger effect sizes seen for birds in flocks from the

west and central regions of the study site, while on the east of the study site the effect of strength was still significant but very small (Table 3.2).

Betweenness was strongly correlated with movement behaviour. Birds that had high betweenness (and thus were important in connecting different social groups) used more sites (in two regions of the study area) and had larger home ranges (Table 3.2).

Degree, strength and betweenness were all found to be predictive of the number of sites used by birds in one year, though there was some regional variation (Table 3.2): high-degree birds were more mobile in terms of site use (movement propensity). The distribution of betweenness within the population was significantly correlated with movement propensity. Most marked birds for which moult site was known in both years showed moult site fidelity (90 site-faithful: 10 moved: 38 unknown), but this fidelity was not correlated with the strength of connections, degree or betweenness, with high degree or betweenness birds showing no pattern in moult-site fidelity (Table 3.2). We did not observe birds changing moult sites within a moult period.

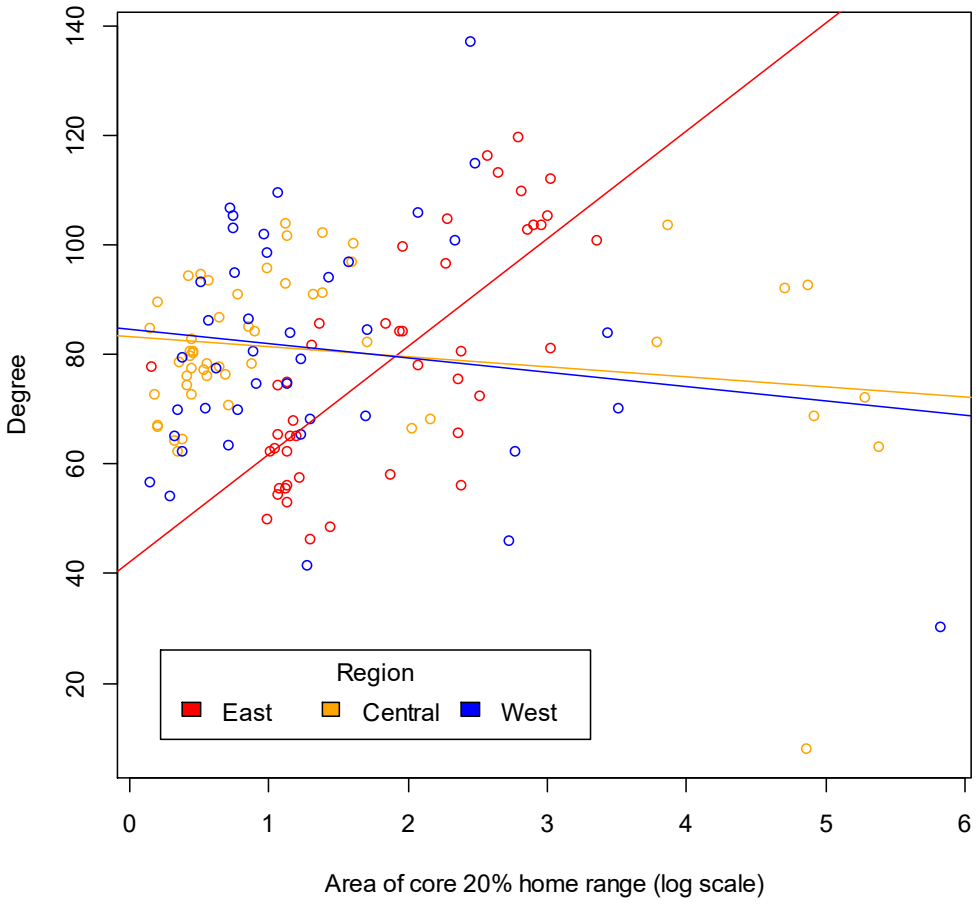


Figure 3.3. The interaction between the geographic location (region) of a flock, movement and degree. Lines are taken from linear models for display purposes only.

Table 3.2. Outputs from double semi-partialling MRQAP (MRQAP-DSP) to identify correlations between matrices of network metrics (degree, betweenness and strength) and three measures of movement propensity (number of sites used, area of core 20% of home range and moult site fidelity) for each of the three geographic regions (n=138). Coefficients with $p<0.05$ are shown in bold.

Response variable	Geographic region	Predictors	Estimate	*P*
Number of sites used	Central R^2=0.214	intercept	-0.2515	0.281
		Degree	**0.0584**	**<0.001**
		Strength	**-0.0095**	**<0.001**
		Betweenness	0.0026	0.280
	East R^2=0.333	intercept	-0.2619	0.274
		Degree	0.0017	0.789
		Strength	**-0.0148**	**<0.001**
		Betweenness	**0.0277**	**<0.001**
	West R^2=0.220	intercept	-0.5164	0.096
		Degree	**0.0448**	**<0.001**
		Strength	**-0.0075**	**<0.001**
		Betweenness	**0.0050**	**0.017**
Home range area (20%)	Central R^2=0.184	intercept	0.1193	0.254
		Degree	**-0.0086**	**0.022**
		Strength	**-0.0015**	**0.001**
		Betweenness	**0.0060**	**<0.001**
	East R^2=0.556	intercept	0.0454	0.293
		Degree	**0.0103**	**<0.001**
		Strength	**-0.0006**	**0.002**
		Betweenness	**0.0021**	**0.002**
	West R^2=0.277	intercept	-0.0527	0.280
		Degree	**-0.0068**	**<0.001**
		Strength	**-0.0011**	**<0.001**
		Betweenness	**0.0057**	**<0.001**
Moult site fidelity	Central R^2=0.0002	Intercept	0.4356	<0.001
		Degree	-0.0028	0.299
		Strength	0.0003	0.244
		Betweenness	0.0002	0.742
	East R^2=-0.0017	intercept	0.5043	<0.001
		Degree	0.0002	0.918

		Strength	-0.0001	0.872
		Betweenness	-0.0004	0.688
	West R^2=0.0073	intercept	0.6171	<0.001
		Degree	0.0015	0.387
		Strength	-0.0001	0.658
		Betweenness	0.0003	0.426

Social network metrics (degree, strength and betweenness) did not differ between males and females for those birds with 10+ resightings in year 1 for whom sex was known (n=107) (F_{5667}=0.902, p=0.439). However, paired and breeding birds differed in their social network metrics to unpaired and non-breeding birds. Paired birds displayed different social network metric profiles to unpaired birds, with the former showing more skewed strength distributions and higher betweenness, but no difference in degree (Table 3.3). Breeding status was predicted by degree and strength matrices, with successful breeders having higher strength and lower degree than those birds that did not breed successfully (Table 3.3). Though significant, the correlation between paired status and betweenness, and that of degree with breeding status, were very weak. However, strength was strongly correlated with both paired and breeding status (Figure 3.4).

Table 3.3. Outputs from double semi-partialling MRQAP (MRQAP-DSP) to identify correlations between matrices of network metrics (degree, betweenness and strength) and both paired and breeding status. Predictors where p<0.001 are shown in bold (n=138).

Response variable	Predictors	Estimate	*P*
Paired status (paired vs unpaired birds)	intercept	0.4619	<0.001
	Degree	-0.0133	0.328
	Strength	**0.3506**	**<0.001**
	Betweenness	**0.0005**	**<0.001**
Breeding status (successful breeders vs non-breeders)	intercept	0.6443	<0.001
	Degree	**-0.1241**	**<0.001**
	Strength	**0.4475**	**<0.001**
	Betweenness	-0.0001	0.548

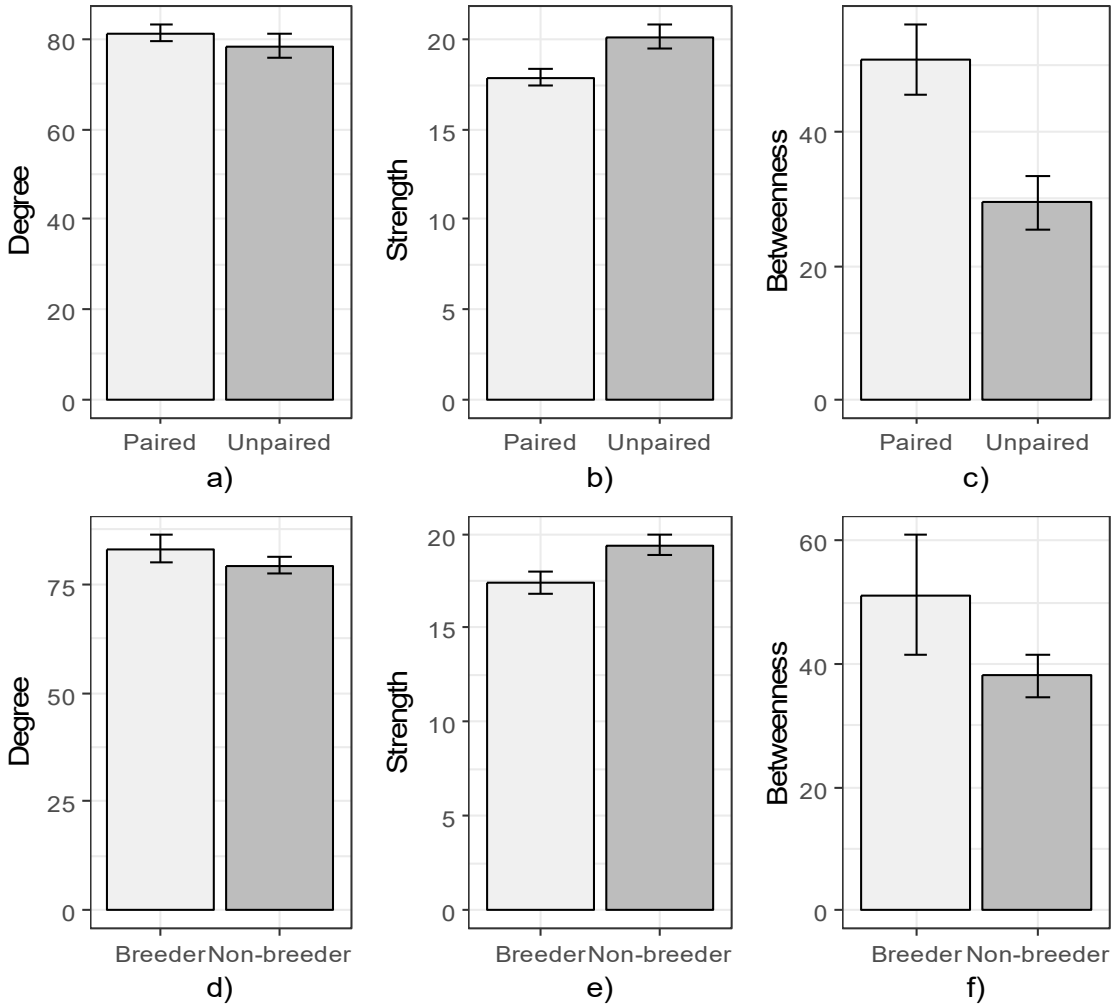


Figure 3.4. Mean social network metrics of paired vs unpaired birds (a-c) and successful breeders vs non-breeders (d-f). Error bars show ±1SE. Paired birds (n=76) were observed defending territory or young together in the breeding or moult season, unpaired birds (n=69) were not. Breeding birds (n=33) were observed with young, either alone or with their pair. Non-breeders (n=112) were not observed with unaccompanied young.

Both paired and unpaired birds have skewed strength distributions; however, paired birds have a more strongly skewed distribution (skewness 1.184 paired vs 0.858 unpaired). Paired birds also showed a higher density of weak connections than unpaired birds (Figure 3.5), and a higher density of very high strength connections (connections above 0.8 half-weight index – individuals appearing together 80% of the time).

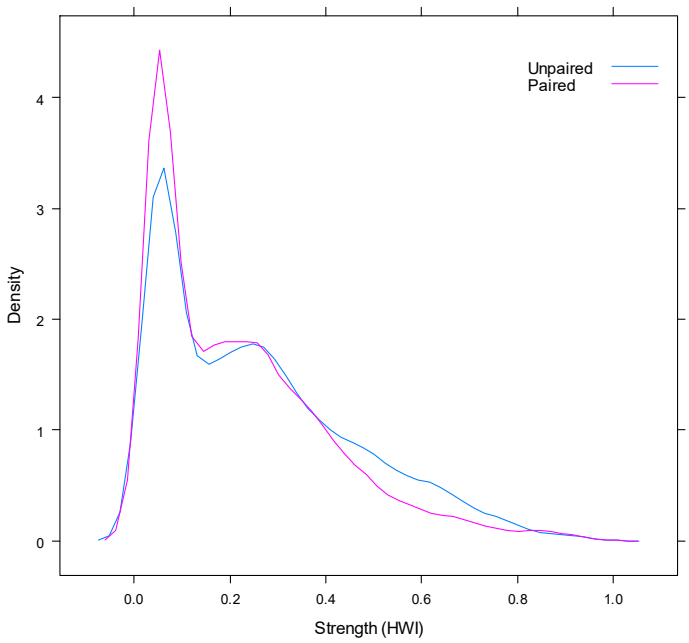


Figure 3.5. Frequency of association strengths for paired and unpaired birds. The peak in associations of a strength of 0.05 for both classes indicates a high proportion of weak connections (birds seen together 5% of the time), with very few connections stronger than 0.6 (birds seen together 60% of the time).

Results of a MRQAP-DSP supported the hypothesis that betweenness does not covary with body condition, with permutations of the data showing covariance in the predicted direction (i.e. that birds that gained condition were those with low betweenness), but with a marginally non-significant effect (n=72), $f_{3,2552}$=40.07, p=0.058. High betweenness birds neither begin the year in poor condition nor show greater changes in condition than low betweenness birds.

Model selection by AICc

Neither condition nor body mass in 2012 were found to predict the number of sites used by birds over the year or their ranging behaviour. The top models selected by AICc contained body condition and paired status (movement propensity and range model selection), an interaction between paired status and body condition (movement propensity model selection only), and sex,

breeding status and weight (range model selection only) but none was found to be a strong or significant predictor of site use or range size.

The number of sites used over the year correlated strongly with change in body condition; with birds that increased in condition (increased scaled mass index) using fewer sites (Table 3.4). The geographic region of each bird's moult site and a factor assigning an ID to both partners within a pair (where both featured in the analysis) were included as random factors in the top model. Breeding and paired status were not retained within the top models. However, the area of the 20% utilisation distribution of the home range was not found to be correlated strongly or significantly with a change in scaled mass index.

Table 3.4. a) Top models (~2 ΔAICc) used in model averaging and b) model averaged coefficients for models correlating change in body condition with movement propensity (number of sites used) over one year (n=70).

a)

Model	df	Log likelihood	AICc	ΔAICc	Weight
Number of sites (fixed effect) + Pair ID (random effect) + geographic region (random effect)	5	-19.17	49.28	0.00	0.75
Number of sites (fixed effect) + Pair ID (random effect) + Moult site 2012 (random effect)	5	-20.28	51.49	2.21	0.25

b)

Model-averaged coefficients: (full average)	Estimate	SE	Adjusted SE	z value	*P*
(Intercept)	0.4515	0.199	0.203	2.230	0.026
Number of sites used	**-0.0612**	**0.023**	**0.023**	**2.616**	**0.009**

3.5 Discussion

Individuals with the potential to be superspreaders of disease, as defined by high degree and betweenness (Rushmore et al. 2014), were identified in the study population. Importantly, these individuals were also found to range further and use more sites than those classified as being at lower risk of acting as superspreaders. Contrary to expectations stemming from an assumed interaction between condition and dominance, potential superspreaders in the social network could not be defined by broad biological classifications based on condition, mass or sex. However, unpaired birds were more likely to occupy social network positions that would allow them to transmit infection to a disproportionately high number of individuals. Neither body condition at the start of the study period nor mass was predictive of movement, thus these parameters could not identify highly mobile birds that could transmit infection widely. However, these highly mobile potential superspreaders did diminish in condition more than less mobile birds.

As predicted, social network metrics in the present study correlated in ways that allowed potential superspreaders to be distinguished from other individuals. Those individuals with high betweenness and high degree could have a disproportionately large effect on the transmission of disease (Rushmore et al. 2014) since they contact not only high numbers of individuals but also individuals from different social groups. The expected negative correlation between strength and betweenness was not found in the present study, suggesting that whilst some high strength birds were making frequent connections within their social group only, others moved amongst groups whilst maintaining strong associations with some associates, possibly related birds (see also Harrison et al 2010). The importance of these correlations between network metrics is that they identify variation between birds that are otherwise similar. Hence, although absolute degree does not vary widely within this population, regardless of sex or breeding class, there is substantial variation in degree, strength and betweenness.

Correlations between network metrics also have an important effect at larger scales. For example, they may reduce network stability (Vasquez et al. 2013), since they suggest increased variance between individual nodes, meaning that they are more differentiated in terms of their roles within the network. This has important implications for the transmission of disease and its management for example by removal of certain individuals. In scale-free networks, a few individuals are very highly connected whilst most others have few connections and are (in network terms) interchangeable (Albert et al. 2002). Since random removal of individuals will mainly remove uninfluential, undifferentiated individuals, scale-free networks are robust to random removals but very vulnerable to targeted removal of highly connected individuals. Conversely, small-world networks (Watts and Strogatz 1998) are characterised by dense clusters of individuals connected in the network by several longer connections between clusters. Here, social groups are visible as clusters, with inter-cluster connections being occasions when individuals move between social groups, or social groups come together. Small-world networks tend to allow infection (or information) to spread very rapidly since many nodes have connections that connect them to both close and distant associates. This means that there are several shortest paths across the network (the often highlighted ‘six degrees of separation’ (Travers and Milgram 1969)) and the network may be equally affected by random or targeted removal of individuals, since there are fewer uninfluential network positions (Albert et al. 2002).

Importantly, in the present study, potential superspreaders (those birds showing high degree and betweenness) had larger home ranges and used more sites. The slightly higher betweenness seen in birds using more sites was expected, given the construction of the network on gambit of the group (in which individuals are deemed associating equally with all others in the group at the observation site (Franks et al. 2010)), and likely reflects that in this free-living non-territorial species, individuals that use several sites encounter more distinct social groups than those using fewer sites. These results also indicate that birds with strong, stable bonds to a small social group (high strength birds) range less far and hence are likely to be of less importance in disease

spread. However, movement patterns and, possibly, the social network may change throughout the year. It will be important to establish the impact of seasonality on variation in movement levels and on the overall structure of the network.

The predicted correlations between social network-based superspreader potential and body size or body condition were not supported by results from the present study. This was surprising given the assortment by size seen in other group-living species (e.g. fish (Hoare et al. 2000; Croft et al. 2005b), and multi-species flocks of passerines (Farine et al. 2012)) and the expected correlations between body size and dominance (Sandell and Smith 1991), condition and dominance (Poisbleau et al. 2006), and dominance and social network position (Bierbach et al. 2014). However, this finding may reflect the abundance of suitable habitat in the study area. The study area contains abundant grassland and water bodies and the population is managed by egg oiling and culling. Thus, it may be that all birds are in reasonable condition since good habitat seems unlikely to be a limiting factor. Whilst condition may not provide a way of identifying potential superspreaders, breeding class appears to be a strong structuring mechanism within the social network. When targeting individuals for disease management, targeting non-breeding birds may have a greater effect in reducing disease transmission.

Paired individuals' high betweenness may demonstrate the importance of the pair unit in goose social systems since it suggests that pairs move between social groups more than unpaired birds. This contrasts with other social systems in which only certain classes of individual roam frequently between groups (e.g. unattached roaming males in *Panthera leo,* the African lion (Craft et al 2011) and *Suricata suricatta*, meerkat (Drewe et al 2009) systems) and those in which dispersal and contact rate is the result of not retaining territory (Fenner et al 2011). Paired Canada geese appear to differ from unpaired individuals in that they have a more binomial distribution of association strengths, with many weak connections and a few strong connections. Unpaired geese have a greater number of moderate associates, with whom

they are observed in 40-70% of observations, than paired birds. Accordingly, in Canada geese, whilst unpaired individuals may be capable of infecting more of their flock, paired individuals may be able to transmit infection to several different flocks.

The findings of the present study have some clear implications for disease management in similarly structured bird populations. Firstly, it is important to recognise that birds are unlikely to be equal in terms of their contribution to the transmission of disease: unpaired birds were shown to contact greater numbers of individuals, and paired birds more social groups. This suggests that effective containment of infection might be best served by the management of non-breeding birds. This would require intervention during the breeding season (at which point flocks are largely formed of failed breeders and non-breeding birds) or early in the moult. More generally, these results identify a small world network, in which the entire network, from cluster to cluster, can be traversed within a few steps. For diseases requiring long exposure for transmission, effective disease containment may be best achieved by the complete removal of any partially infected social clusters, with minimal disruption to neighbouring clusters, rather than removing a set percentage of the population indiscriminately. These preliminary findings are based on a stable, undisturbed network. For disease management options to be properly evaluated, managers require information about the consequences of network perturbation on network structure.

In conclusion, this study identified correlations between social network metrics which identify a class of birds that have the potential to act as superspreaders within this population. However, expected correlations between movement and social network metrics varied in relation to breeding status. Breeding birds are likely to present the lowest relative threat to the population as superspreaders, since they are in frequent contact with fewer birds. It is then important to distinguish between the remaining population to assess whether likely superspreaders are those that appear frequently in large groups (Godfrey et al. 2006), those travelling between groups (Craft et al. 2011) or

those that range over a greater area (Drewe 2010; Fenner et al. 2011; Weber et al. 2012) taking into account seasonality.

4. Homophily in goose social networks: how does biological variation scale within social groups?

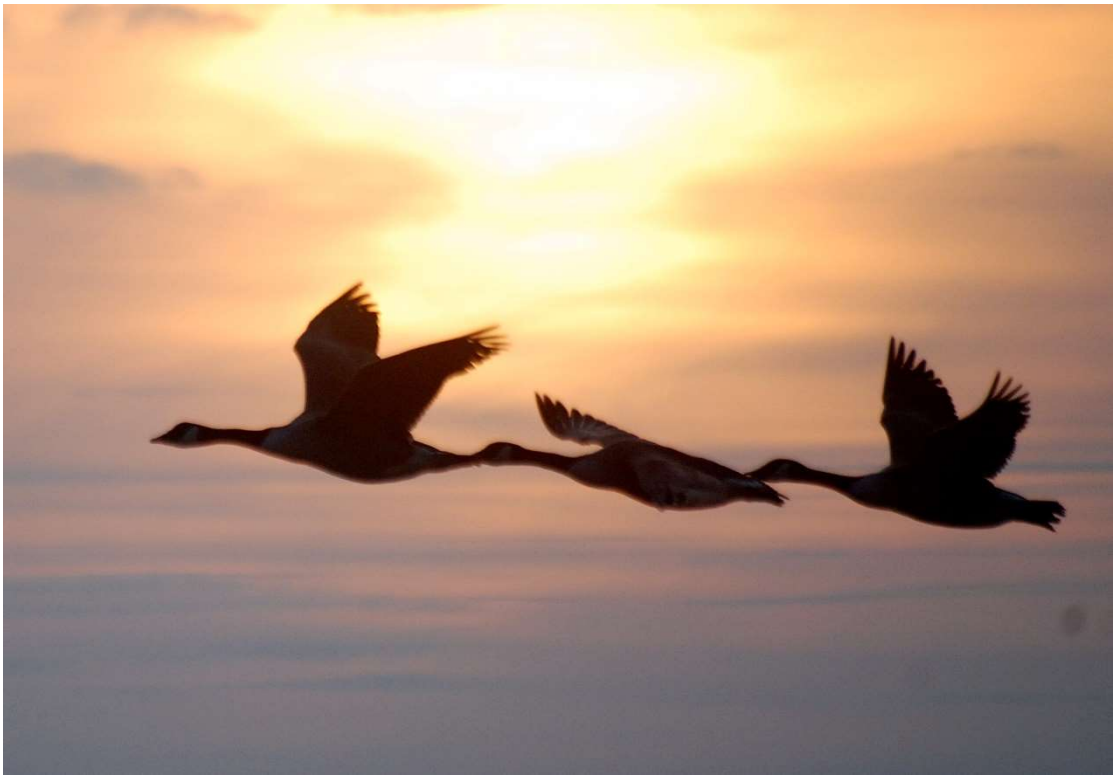


Photo credit: Matthew J Silk

4.1 Abstract

How ‘individual’ are individuals? Similar individuals may choose to associate - ‘birds of a feather flock together’ - with affiliation based on phenotype, kinship or condition. On the other hand, individuals in the same social circle may become more similar, having been exposed to the same conditions. Many species are capable of maintaining relationships at several social scales: close relationships to their breeding pair and immediate family, looser connections to their social group and the wider population. These levels of social circle are conserved and can be observed in species from geese to elephants. Whilst similarity within connected groups (homophily) has been studied at multiple scales in humans, studies in animals are largely limited to identifying assortative mating. This study goes beyond the breeding pair to examine homophily at multiple social scales. This study found that breeding pairs were distinctively strongly connected within pre-breeding networks and were frequently observed as nearest neighbours in the field. Birds’ movement behaviour was more similar to that of their social group than that of birds in other social groups and the more frequently birds associated, the stronger was this relationship. This was not an artefact: frequently associating dyads used ranges of similar sizes but without their ranges necessarily overlapping greatly. Homophily was detected in simulated pairs and family groups but not in simulated small flocks (of 16 birds) or large flocks (of 60 birds). Different social groups also showed different movement and condition profiles. There was a longitudinal cline in body condition, with birds on the west of the study area losing condition and social groups in the east gaining condition. Since groups in poorer condition may be more susceptible to greater morbidity or mortality in the event of a disease outbreak, establishing the level of homophily within the network adds an extra layer of information in predicting the outcomes of infection in different social groups. Where homophily is strong, knowing an individual’s behaviour may also allow for the careful extrapolation of that trait to its social group.

4.2 Introduction

Though many species are acknowledged to display some form of social living, from seasonal sociality to colonialism to eusociality, the mechanisms governing group formation and maintenance, from information use (Firth et al. 2016) to the importance of consensus in group cohesion (Miller et al. 2013) are still being uncovered (Fawcett et al. 2014; Silk et al. 2014). Social encounters are likely to be non-random either through accident (e.g. site fidelity (Kruckenberg and Borbach-Jaene 2004; Willis and Brigham 2004; Glover and Altringham 2008; Harrison et al. 2010b; Wakefield et al. 2015)) or choice (Peuhkuri 1997; Jiang et al. 2013; Martin 2013), causing subsections of the population to spend more time together than with the population at large. Different trait combinations arise from this incomplete mixing and may contribute to the group developing a unique 'phenotype' (Planas-Sitja I, Deneubourg J-L, Gibon C 2015; Farine et al. 2015c), either as a cause or a consequence of their group membership. Aside from evidence of assortment by size in shoaling fish (Krause et al. 1998; Hoare et al. 2000; Croft et al. 2003), there has been little explicit research in animals on assortment by trait above the level of breeding pair. Such assortment would result in individuals forming groups on trait lines (homophily) and encourage the development of groups with characteristic traits or behaviours (Mann et al. 2012). These groups may then respond differently when faced with the same ecological pressure (Planas-Sitja I, Deneubourg J-L, Gibon C 2015). Research on the extent and the strength of homophily shown within animal social groups is vanishingly scarce. Social network analysis, which quantifies the contact rate between every two individuals (or dyad) within a population, provides a robust way in which to establish the extent of homophily in social animals, and so look for assortment in complex and dynamic social structures beyond assortative mating.

In many instances, animals living in groups may share similar phenotypic traits either as a cause or consequence of group membership. Homophily is the term used in sociology when connections form preferentially between similar individuals (McPherson et al. 2001). Aristotle and Plato remarked upon

humans' homophilous tendencies, with homophily recorded in social groups on race, value and lines (McPherson et al. 2001). Homophily has been recorded frequently in animal systems, under various guises. Assortative mating is extremely widespread, having been observed in five phyla and from protists to mammals (Jiang et al. 2013). Assortative shoaling (Krause et al. 1996; Peuhkuri 1997; Croft et al. 2005b) has been suggested to lessen the oddity effect (in which odd individuals that differ in appearance to the rest of their group are more noticeable and therefore potentially at greater risk of predation (Croft et al. 2009a; Rodgers et al. 2011; Rodgers et al. 2014)). Even within social groups, age and sexual homophily can dictate associations (Lusseau and Newman 2004; Pace et al. 2011; Hirsch et al. 2012). In pukeko (*Porphyrio melanotus melanotus*), homophily in breeding networks suggests that most interactions are between individuals of the same sex competing for breeding opportunities (Dey and Quinn 2014). However, similarity to one's associates may also be a consequence of group living. In many species there will be incomplete mixing (driven by spatial constraints, territorial behaviour or dispersal strategies), meaning that individuals from the same group are more highly related to each other than to others in the population (Wolf et al. 2007; Harrison et al. 2010b). Related individuals will have similar genotypes, phenotypes and may react similarly to external stresses. Finally, individuals within a group are also more likely to be subject to the same ecological stresses (Dodson 1989) and environmental conditions (Semmens et al. 2009; Feil and Fraga 2012) than individuals from two geographically distinct groups.

Homophily, however it arises, creates groups of similar individuals; groups with a distinct phenotype (Kondrashov and Shpak 1998; Farine et al. 2015c). Groups may show distinct natures (e.g. high movement (Craft et al. 2011)) or cultures (Mann et al. 2012; Allen et al. 2013; Cantor et al. 2015). Although previous research has found evidence for both homophily (Lusseau and Newman 2004; Croft et al. 2009b; Mann et al. 2012) and heterophily (Vercken et al. 2012; Keiser et al. 2016) in natural systems, very little is known of the implications of homophily and group phenotypic composition for higher processes, such as the transmission of information or disease. Where groups differ greatly in their characteristics (as a result of wide variation in the

population and strong homophily), knowing the precise phenotype of each group becomes important when predicting population-level processes, such as the transmission of disease. In meerkats, *Suricata suricatta*, both diurnal behaviour patterns (Thornton et al. 2010), which may influence exposure to disease, and bacterial communities (Leclaire et al. 2014), which may influence infection and disease severity (Paull et al. 2012; Vaumourin et al. 2015), are specific to the social group. In the Serengeti lion (*Panthera leo)*, group formation is based on age and sex, and movement patterns vary between these types of pride (Craft et al. 2011). Even disease status matters: stickleback shoaling patterns were found to be affected by infection status, with healthy shoals avoiding sick fish (Croft et al. 2011a; Rahn et al. 2015). Thus, the phenotype of the group may influence its role in disease transmission and morbidity in the event of infection.

Animals may seek out similar individuals with whom to form groups. They may become more similar to their associates because of their exposure to similar conditions. However, there are circumstances in which the group may become less homogeneous: i) when rare phenotypes are favoured and ii) when the group has a strong hierarchy. If phenotypes are favoured only if rare, there is a strong pressure for groups to show heterophily, through dispersal if necessary (Vercken et al. 2012). Within-group hierarchies, through mechanisms such as competition interference (Vahl et al. 2005; Bijleveld et al. 2012) and social vigilance (Favreau et al. 2010), may also distort the simple prediction of homophily within groups (Dey and Quinn 2014), however this has not been tested empirically. Linear hierarchies may lead to heterophily in groups, with low-ranking individuals consistently in poorer condition than high-ranking individuals, whatever the resources available (Fan et al. 2015). Individuals may associate frequently and yet show distinctly different movement patterns: one individual may be resident at a site, with the other a frequent visitor with a much larger home range. Social network analysis, when combined with home range analysis, allows this relationship to be distinguished from the dyad that moves in tandem.

How might homophily arise in biological parameters that impact disease transmission, such as condition and movement? The advent of information on contact rates between individuals (within and between social groups) has greatly advanced our understanding of disease transmission in wild animal systems (Böhm et al. 2008; Hamede et al. 2009; Bull et al. 2012; Drewe et al. 2013; Weber et al. 2013; Reynolds et al. 2015). However, the complementary information on how individual phenotypes contribute to group-level phenotypes is poorly understood. Without this, there can be no appreciation of the true biological impact of pathogen transmission (Farine et al. 2015c). Condition is frequently assortative in breeding pairs (Heitmeyer 1995; Masello and Quillfeldt 2003; Jawor et al. 2003). If groups show homophily in body condition, then all members of a group will be in similar condition (Choudhury et al. 1996). This in turn leads to a population comprising groups where all individuals are either in poor condition or in good condition. If other mechanisms (for example dominance hierarchies) determine the distribution of resources within a group, there will be heterogeneity of condition within each group. Since body condition can predict how an individual responds to infection (Beldomenico et al. 2009; Höner et al. 2012), the impact of the pathogen infecting one social group may be very different to that of it infecting a neighbouring group if groups differ in condition. Groups would be expected to show homophily in movement since a prerequisite of social connection is being present together; however, there has been little research into the extent to which social groups show characteristic movement patterns or members' similarity in movement levels, despite its importance in disease transmission (Craft and Caillaud 2011; Fenner et al. 2011; Lopes et al. 2016).

Canada geese (*Branta canadensis)* present an ideal study system in which to explore the relationship between association strength and homophily in movement levels and condition. Geese have a structured social system with dominance based upon group size (with families dominant over breeding pairs, and breeding pairs dominant over unpaired birds (Poisbleau et al. 2006)) and the mere presence of family members can improve males' performance in agonistic encounters (Scheiber et al. 2009). There is support for homophily, with breeding pairs showing synchronised body condition

(Choudhury et al. 1996), an effect also seen at the family level in other avian species (Royle et al. 2012). Canada geese are extremely social and show enormous variation in flock sizes depending on the season and environmental conditions, with groups ranging in size from breeding pairs to wintering flocks of hundreds. In addition to this, Canada geese are a potential reservoir of the virulent herpesvirus duck plague, high pathogenicity avian influenza, low pathogenic *E. coli* and *Salmonella* species (Bonner et al. 2004; Tsiodras et al. 2008). They are common (62,000 breeding pairs in summer in the United Kingdom, (Holt et al. 2015)), widely distributed and frequently use sites also used by humans, domestic animals and migratory species. For these reasons, it is important to understand fully factors that might impact disease transmission in these populations.

This study is the first to look at trait homophily in birds above the level of breeding pair and the first in any species to examine how this scales with widening social circles. It establishes whether goose social groups can be said to have a phenotype and what this means for the transmission of disease in a highly mobile species. Frequent associates were predicted to show homophily in their ranging behaviour, movement propensity since they would be expected to use the same sites over the same area. However, frequent associates may show heterophily in body condition above the level of the breeding pair since the need to maintain social vigilance may mean that less dominant birds are in poorer condition. The social network measure *strength*, which captures the number of times each dyad was seen together versus apart over a given period, was used to quantify frequency of association. Correlative analyses were used to test the relationship between how frequently individuals' associated, any breeding relationship and their similarity in body condition and home range. These sought to test whether frequent associates show similar movement levels at a population level, as well as establish whether social groups are homogeneous with regards to body condition (as predicted from studies of assortative mating (Jiang et al. 2013)) or heterogeneous (as would be the case if resources are portioned within the group according to rank). Since many social species have several circles of association (their mate, their family, their familiar associates), we

also sought to establish the levels of homophily at each of these widening social circles (Hill et al. 2008; Borg et al. 2015), and at what point this relationship between homophily and association strength (if present) declines. The importance of the pair and family are acknowledged in the goose social system (Lamprecht 1986; Poisbleau et al. 2006; Poisbleau et al. 2008) and homophily in body condition and movement behaviour at these levels can be predicted. However, homophily in condition and movement beyond the level of the family would suggest that geese maintain social bonds with a larger social group than has been demonstrated previously.

4.3 Methods

Study system

The study area comprised the Cotswold Water Park (Ordnance Survey grid reference SU 0796), an area of flooded and working gravel quarries surrounded by farmland in southern England, UK. Canada geese (*Branta canadensis*) are resident at this site all year round with a wintering population in excess of 600 individuals (Holt et al. 2015). Flock sizes and composition change seasonally, with the largest flocks appearing in winter when geese aggregate to forage on pasture (mean flock size in winter 2012= 69 birds, range=2-305). Canada geese are highly social and it is very unusual to see individuals alone. They have been frequently observed to roost and forage alongside native greylag geese (*Anser anser)* in this area, and hybrids have been observed, though flocks tend to separate on species lines when moving around or between sites. All analyses, other than that looking at winter association strengths of paired and unpaired birds are based on data collected over a full year.

Canada geese moult following breeding, leaving them flightless in much of May, June and into July, when entire flocks can be caught. In July 2012 and 2013, geese were caught at moult sites within the water park. Entire flocks

were rounded up on the water by an experienced team of kayakers and driven from the water into a screened pen. Individual birds were fitted with highly visible neck collars bearing unique codes and metal British Trust for Ornithology leg rings in accordance with local ringing practices (2012=174 birds caught, 153 collars fitted; 2013=189 birds caught including one too young to be ringed, 35 new collars fitted). Neck collars (dimensions: inner diameter = 42mm, height = 65mm) were produced by Interrex and were formed of black plastic overlaid with orange, so that the two-letter codes appeared as black text on an orange background. In 2012, sex was established for 115 birds by cloacal examination performed by experienced staff (Hanson 1962). Staff competent in sexing were not present at all catches, hence not all birds were sexed. This method entails eversion of the cloaca to detect the presence or absence of the penis and is estimated to carry an error rate approaching 15%, which is biased towards the miscategorisation of males as females (Cooch et al. 1996). In 2012, biometrics were recorded for all adult birds (n=153). In 2013, biometrics were recorded for recaptured adult birds marked in 2012 (n=72). Each adult bird was weighed in a hessian sack suspended from a zeroed spring scale (Pesola©) measuring mass to the nearest 10 grams. Biometrics - skull (head and beak) and tarsometatarsus bone (hereafter tarsus) length - were measured with callipers to the nearest millimetre (Black et al. 2014).

Assignment of breeding and nearest neighbour status

Breeding pair status was assigned to adults that were observed to be defending territory or offspring in February-August in the year of interest. On the basis that birds are more familiar with the birds close to them in the flock whilst foraging or roosting, each bird's 'nearest neighbour' was recorded when flocks were largely stationary on land. During nearest neighbour classification, the flock was scanned from left to right, and each identifiable bird's nearest marked neighbour was recorded, along with the approximate distance (in goose body lengths) between birds. If the focal bird's nearest neighbour was unmarked, both the distance to the unmarked bird and that to the nearest marked bird were recorded. If the focal bird was equidistant between two

birds, the identity of and distance to both were recorded. Nearest neighbour observations were recorded throughout the year, though only when birds were clearly identifiable and on land.

Construction of the networks

Collar codes of marked individuals were recorded in the field by an observer with binoculars and a telescope. Group membership, location, flock size, time and date were also recorded. A total of 390 flock resightings were gathered over the year. Resightings took place on 146 days between July 2012 and June 2013, resighting in every month of the year and from dawn until dusk. Birds in a flock present at the same site at the same time were judged to be associating, an assumption that is termed “gambit of the group” (Whitehead and Dufault 1999; Franks et al. 2010), and each of these group associations was termed an ‘event’. The extent of flock membership was determined by a chain rule based upon local geography and the distances between birds – birds were considered to be within a flock if they were in visual contact, were not separated by barriers such as hedges or by distances four times greater than the mean inter-individual distance (measured in goose body-lengths to allow accurate calculation of estimates at distance). On water bodies, all individuals present on the lake were termed associating. In the field, groups of geese tended to stay away from field margins or boundaries and self-organised into cohesive flocks. If a group of birds joined or left a flock in which all marked individuals had been identified, the moving group was recorded both as part of the large flock and as a subunit in a separate ‘event’ to reflect the group membership choice made by the individuals involved. Association matrices were constructed using the half-weight index to record association strength. The half-weight index is commonly used in social network analysis for the construction of social networks where nodes are more likely to be observed when not associated, or when not all individuals can be identified (Whitehead 2008). The half-weight index assigns each dyad an association strength based upon the number of times they are seen together (x) versus separately in different periods (y_A+y_B) or separately in the same period (y_{AB}).

$$\text{Half-weight index} = x/(x+y_{AB}+1/2*(y_A+y_B))$$

Though breeding pairs are expected to associate strongly throughout the year, this is predicted to be most clearly seen first in the breeding season, when birds frequently appear as pairs, and secondly during the post-moult period when they frequently appear in small flocks of 6-20 (equivalent to 1-3 families).

Calculation of social network metrics

Association matrices, networks and metrics were calculated based upon the full year of resightings except in the analysis of paired birds' winter connection strength. In this analysis, connection strengths were calculated from networks based on resightings of birds from 1st November 2012 to 26th February 2013 only (1523 resightings of 142 birds). The whole-year networks mask seasonal variation and look for overall patterns of association, whilst the winter network from which connection strength was calculated focuses explicitly on associations outside of the breeding season and when flock sizes are largest. Strength was calculated in R (version 3.2.0 (R Core Team 2013), package 'sna' (Butts 2007)) for birds with 10 or more resightings (n=145) since it was at this point that variation in the relationship between number of observations and metrics ceased to increase (see chapter 1). Strength is number of associates weighted by the number of associations and can increase in two ways: by increasing the number of associates, or by associating more frequently with those associates (Whitehead 2008). Strength was corrected for number of observations by regression calibration: recalculation from residuals of an ordinary least squares regression of number of observations on each network measure for birds that had been resighted at least ten times (Rosner et al. 2006).

Clustering algorithm

The walktrap algorithm (R, version 3.2.1, package 'igraph' (Csardi and Tamas 2006)) was used to assign individuals to social clusters or 'communities' representing social groups, based on their position in the social network (Pons

and Latapy 2005). Dyads were classified as containing both members of the same breeding pair, members of the same social group or members of different social groups to form a three-level categorical variable of dyad type.

Calculation of scaled mass index, a proxy of body condition

Body condition, as a composite outcome of the individual's resource acquisition and energy expenditure, was predicted to be more similar between birds that associated more frequently. Scaled mass index, a proxy of body condition, based on skull length and mass, was calculated after Peig and Green from biometrics recorded during the moult catches (June 2012 and 2013). In this calculation, biometrics (here mass, M_i, length, L_i and an arbitrary value of L, L_0) are scaled by b_{SMA}, the slope of the standard major axis regression of the biometric L to give ˆMi, which is the predicted body mass for individual *i* when the linear body measure is standardised to L_0 (Peig and Green 2009). This scales the mass of all individuals to that expected for a given body size and is, therefore, dependent on the sample of the population measured. Scaled mass in each year of the dataset thus refers to a single measurement recorded at the time of capture. Association observations were made over 12 months (July 2012-June 2013). In order to calculate the change in scaled mass index between years, all measurements from birds captured in both years were combined into a single dataset. The slope of the relationship and the standard major axis were recalculated and birds were indexed according to their position in this dataset in both years.

$$\text{scaled mass index: } \hat{M}_i = M_i \left[\frac{L_0}{L_i}\right]^{b_{SMA}}$$

Calculation of movement behaviour

Movement behaviour was predicted to be more similar between birds that associated more frequently. Movement behaviour was assessed in two ways to explore movement at fine and large scales. Firstly, the number of sites used by each bird over the year was calculated, useful at a small scale for

distinguishing between birds that frequently moved between geographically close but separate lakes. This value was normalised by taking the residuals from a regression of number of sites/number of observations and adding them to the mean, resulting in a corrected value giving the number of sites used for the known number of observations. Secondly, each bird's core home range was calculated to give a better understanding of the area used by each bird over the year. Home ranges were calculated by assigning latitudes and longitudes to all observations of each bird. These points were then used to calculate utilisation distribution kernel estimations (Worton 1989) in R (version 3.2.0, package adehabitat (Calenge 2006)), which calculates not only the total home range but also the core percentage of the kernel used (i.e. the percentage of the range used most heavily) since the area used by the birds tended to be strongly focused around one or two main sites. In line with previous research (Baracchi and Cini 2014), utilisation distribution home range kernels at the 20%, 50% and 95% levels were calculated, but variation at the higher levels was skewed by the presence of outliers, which was not the case at the 20% utilisation distribution level. Using the 20% utilisation distribution ensured that what was being examined was the individual's habitual core range (Vokoun 2003). Use of the two different movement measures (number of sites versus home range) allowed both birds that only used a few sites in a small area (where home range calculation becomes computationally difficult) and birds using large home ranges to be analysed.

Homophily at wider social circles

Geese associate in pairs, in family groups (Poisbleau et al. 2006) and in flocks that range from fewer than ten individuals to several hundred. In order to establish how homophily scales with these widening social circles, it is necessary to ask whether the biological variation seen between each cluster is greater than the variation seen within each cluster: i.e. if variation between families is greater than that within families. Ranking associations by strength identifies each individual's most frequent associates and allows the creation of theoretical social groups where the true relatedness is unknown.

A histogram of observed flock sizes was used to set five levels of social cluster: partner (number of members=2), family (n=6), small flock (n=16), large flock (n=60) and population. These divisions follow the group size increases with widening social circles seen in other species (Hill et al. 2008). An edgelist was created giving the connection strengths between every two birds within the network. Each bird's strongest connection was labelled their partner or 'pair', the five strongest connections as their 'family', the 15 strongest connections as their 'small flock' etc. These classifications were nested, i.e. each bird's pair was also part of its family. The mean and standard deviation of each biological variable (Table 4.1) within and between each group was then calculated at each social level (pair, family, small flock and large flock). Birds within the same family or small flock were predicted to show smaller differences in these biological variables than birds from different family units.

Table 4.1. Variables used in the exploration of homophily in widening social circles.

Variable	Description
Corrected number of sites used	The number of sites used by the focal bird between July 2012 and July 2013, corrected for the number of observations of that bird.
Core 20% home range area	The area of the 20% core of the utilisation distribution used by the focal bird between July 2012 and July 2013.
Body condition (2012)	The scaled mass index of the bird, giving condition relative to the population, based on biometrics recorded in July 2012.

Statistical analysis

A Mantel test (a matrix permutation analysis) was used to investigate whether breeding pairs were frequently observed to remain close to each other in flocks. Each bird's 'nearest neighbour' was recorded when flocks were largely

stationary on land and used to construct a weighted matrix of nearest neighbour connections. This was correlated with a binary matrix of breeding pair connections (analysis run in R, version 3.2.1, package ‘vegan’ (Oksanen et al. 2015)).

To summarise, bootstrapped linear models were used to identify whether paired birds showed distinctively strong bonds to their breeding pair. Linear mixed models were used to analyse independent data and ask a) whether inter-cluster variation in movement behaviour or initial body condition exceeded intra-cluster variation in social clusters (assigned using the walktrap community detection algorithm); b) whether social groups (assigned using the walktrap algorithm) differed in movement behaviour and body condition. Permutation linear models were used to ask whether intra-cluster variation in simulated networks equalled inter-cluster variation.

Bootstrapping and associated linear mixed models were used to create null datasets and test whether paired birds’ connections to their breeding partner were distinctive. In bootstrapping, values from a distribution are resampled with replacement to generate an approximate sampling distribution of an estimate, from which descriptive statistics can then be calculated (Davison and Hinkley 1997). With the non-independence of data points and frequent departures from normality, bootstrapping and other permutation tests are often used in the analysis of network data (Croft et al. 2004; Farine and Whitehead 2015).

In the analysis of paired birds’ winter connection strength, an edgelist of all winter connections between birds was annotated with whether that connection was between the two partners of a pair (‘pair’), between a paired bird and an associate with which it was not paired (‘other’) or between two birds that were both unpaired (‘unpaired’). This edgelist was then divided into two edgelists: one of the connections of paired birds (to their pairs and to all other associates) and the other of the connections of unpaired birds (the null dataset). Edgelists were identical in their variation in strength, though the edgelist of unpaired birds was larger (5216 entries to the paired edgelist’s

3022). A dummy variable was created within the null dataset to label connections arbitrarily as either ‘pair’ or ‘other’ in the same ratio to that seen in the paired dataset of 68:1, ‘other’:’pair’. An identical bootstrapping procedure (run in R, version 3.2.1, package ‘boot’ (Canty and Ripley 2012)) was then performed on both the paired (observed) and the unpaired (null) datasets to resample from connections labelled as paired and those labelled as other. Datasets were resampled 2000 times and a linear mixed model (version 3.2.1, package ‘lme4’ (Bates et al. 2015)) was run on each bootstrapped distribution to establish whether type of connection (pair/other) predicted connection strength better than a model without predictive terms. Pair ID (a factor linking each member of an observed or null pair) was included as a random factor.

Linear mixed models run in R (version 3.2.1, package ‘lme4’ (Bates et al. 2015)) were used to explore differences in the variation in movement behaviour (number of sites used and 20% home range utilisation) and body condition (difference in 2012 scaled mass) seen between and within dyads from the same breeding pair, dyads from the same social group (social cluster, defined using the walktrap algorithm) and dyads from different social groups. ANOVAs were performed on these models to gauge the variance of the data (for explanatory terms used in these models, see Table 4.2).

Linear mixed models were also used to examine the differences in mean home range area (20% utilisation distribution), number of sites used and 2012/2013/Δ body condition for each of the five social groups delimited using the walktrap algorithm. In these, the ID of the social group was used to predict variation in movement and condition.

Table 4.2. Terms used in linear mixed models of intra- vs inter-cluster variation.

Model	Terms	Type	
Difference in number of sites (log)	Type of dyad	Predictor	Fixed
	Pair ID	-	Random
	ID of recipient in dyad	-	Random
Difference in home range area (log)	Type of dyad	Predictor	Fixed
	Pair ID	-	Random
	ID of recipient in dyad	-	Random
Difference in body condition	Type of dyad	Predictor	Fixed
	Sex of focal in dyad	Predictor	Fixed
	Type of dyad*sex	Predictor	Fixed
	Pair ID	-	Random
	ID of recipient in dyad	-	Random

Permutation linear mixed models were used to estimate homophily in the simulated pairs, families and flocks for the number of sites used throughout the year, 20% core home range area and body condition in 2012. The variation within each cluster (e.g. simulated 'family' 1) was compared with the variation between each cluster (i.e. the variation between family 1 and family 2, family 3…n). Permutation models, chosen due to the possible non-independence of data, were run with the additional use of packages 'lmerTest' (SAS Institute 1978; Schaalje et al. 2002), 'arm' (Gelman and Hill 2006) and 'pbkrtest' (Halekoh and Højsgaard 2014). The type of variation (whether it was intra- or inter-cluster) was predicted to correlate with the standard deviation, with lower deviation between those that were more similar (e.g. birds in the same 'family'). Group ID (nested within the social circle level) was present in models as a random factor.

Ethics Statement

All work was carried out in the UK in accordance with University of Exeter and AHVLA Ethics guidelines and under Natural England and British Trust for Ornithology licences. All field procedures were approved by the University of Exeter Ethics and Health and Safety Committees. All work was carried out with land owners' permission.

4.4 Results

Similarity of paired birds

Paired birds were confirmed to show distinctively strong connections to their partner in the winter preceding their breeding (Figure 4.1a), $p<0.001$ on 2000 permutations. Unpaired birds (the null dataset) showed similar association strengths to both ‘pair’ and ‘non-pair’ connections (Figure 4.1b), $p=0.28$ on 2000 permutations. Variances differed between the distributions as a result of differing dataset sizes: sampling from smaller datasets resulted in rare connection strengths being sampled more frequently and yielded a broader distribution profile.

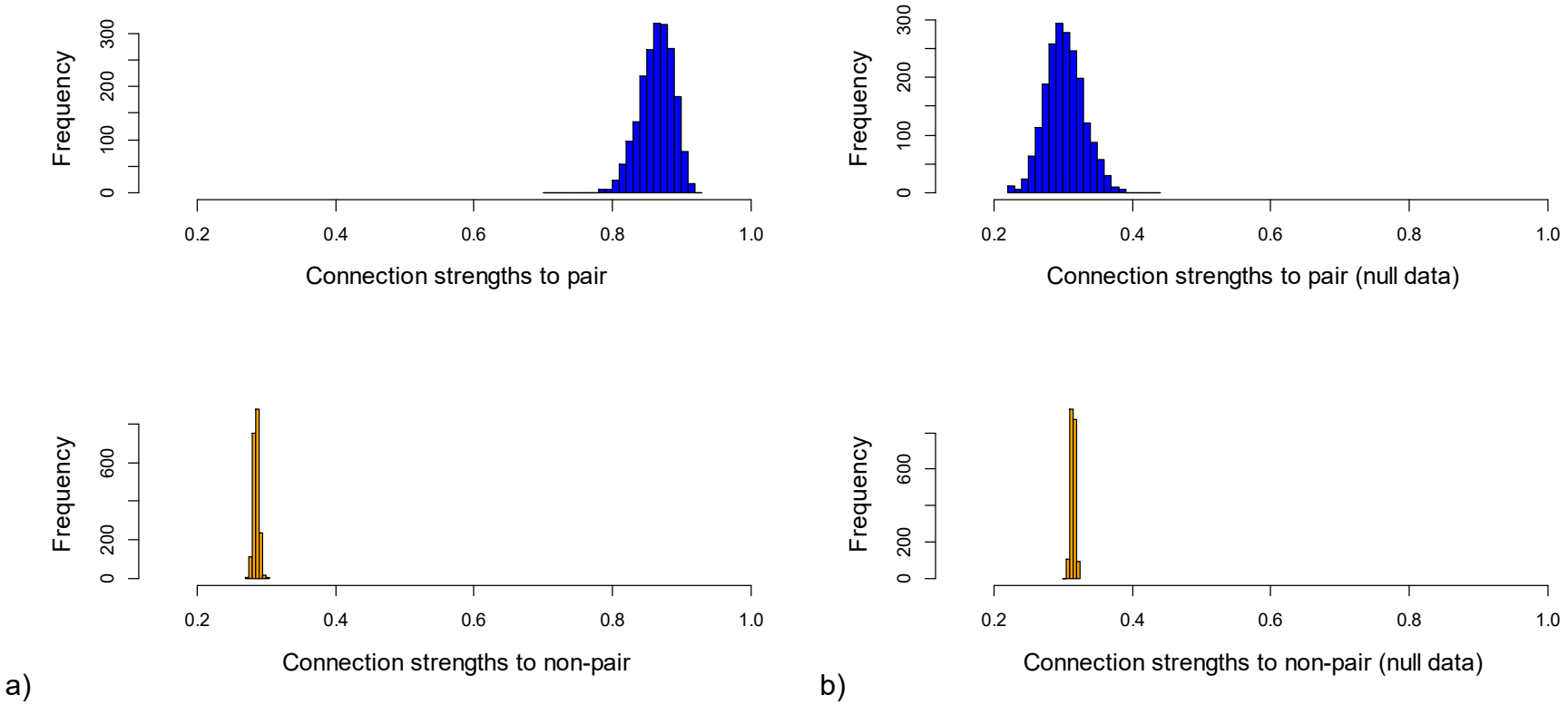


Figure 4.1. Distributions of mean connection strength taken from bootstrapped datasets of a) the true dataset in which type of connection reflects observed behaviour, and b) the null dataset in which the label denoting type of connection was randomly allocated. Distributions of connection strengths to birds classified as pair are shown in blue and to non-pair in orange.

There was a strong correlation between the classification of nearest neighbour and breeding pair membership (Mantel test, r=0.5499, p=0.001). Breeding partners were often, though not always, the focal bird's nearest neighbour. Individuals had more recorded nearest neighbours (range 1-8) than breeding partners (maximum of one).

Examination of the model estimates suggests that, in the summer preceding breeding, paired birds were more similar in body condition to their mate than to birds within their social group, or to group-mates than the wider population (Table 4.3). The mean difference in body condition between pairs is less than that between dyads drawn from the population. However, social relationship (paired, belonging to the same social group or to different social groups) was not predictive of body condition ($F_{2, 8.929}$=0.889, p=0.445). Sex was not retained in the final models.

The closeness of the dyad's relationship strongly correlated in linear mixed models with homophily in movement behaviour. Dyads of birds from the same breeding pair showed significantly smaller differences in their movement propensity and home range area (Table 4.3) than dyads of birds from the same social group, or dyads from different social groups. Whether the dyad were paired, groupmates or in different social groups predicted their similarity in movement propensity ($F_{2, 11.366}$=66.943, p<0.001) and ranging area ($F_{2, 11.806}$=268.61, p<0.001) in linear mixed models.

Table 4.3. Least-squares means of model coefficients for models of movement and condition predicted by dyad type. Coefficients significant at p<0.05 are shown in bold.

Model	Dyad type	Estimate	SE	DF	t-value	Confidence intervals (5-95%)	p
Difference in body condition (2012)	Dyad: same social group	0.497	0.129	0.9	3.84	-1.425-2.419	0.2
	Dyad: different social groups	0.510	0.129	0.9	3.94	-1.423-2.444	0.2
	Dyad: breeding pair	**0.431**	**0.061**	**33.8**	**7.05**	**0.306-0.555**	**<0.001**
Difference in number of sites	**Dyad: same social group**	**0.934**	**0.323**	**6.2**	**2.89**	**0.151-1.717**	**0.03**
	Dyad: different social groups	**1.024**	**0.323**	**6.2**	**3.17**	**0.241-1.808**	**0.02**
	Dyad: breeding pair	**0.583**	**0.091**	**28.4**	**6.42**	**0.397-0.769**	**<0.001**
Difference in home range area	Dyad: same social group	0.319	0.173	6.5	1.84	-0.097-0.736	0.111
	Dyad: different social groups	0.415	0.173	6.5	2.39	-0.002-0.831	0.051
	Dyad: breeding pair	**0.152**	**0.049**	**30.1**	**3.07**	**0.050-0.250**	**0.004**

The more strongly a dyad associated, the more similar the size of their home range, independent of whether they were within a breeding pair. Since birds would by default co-occur in order to associate, similarities in home range size would be purely confirmatory of the dyad's association status, were it not for the absence of a relationship between overlap and association strength (Figure 4.2). This illustrates that even dyads with association strengths of 0.8, birds that spend 80% of their time together, use ranges of similar sizes but may show very little range overlap. These dyads are likely to be frequently resighted together in the small area of overlap of their otherwise entirely separate ranges.

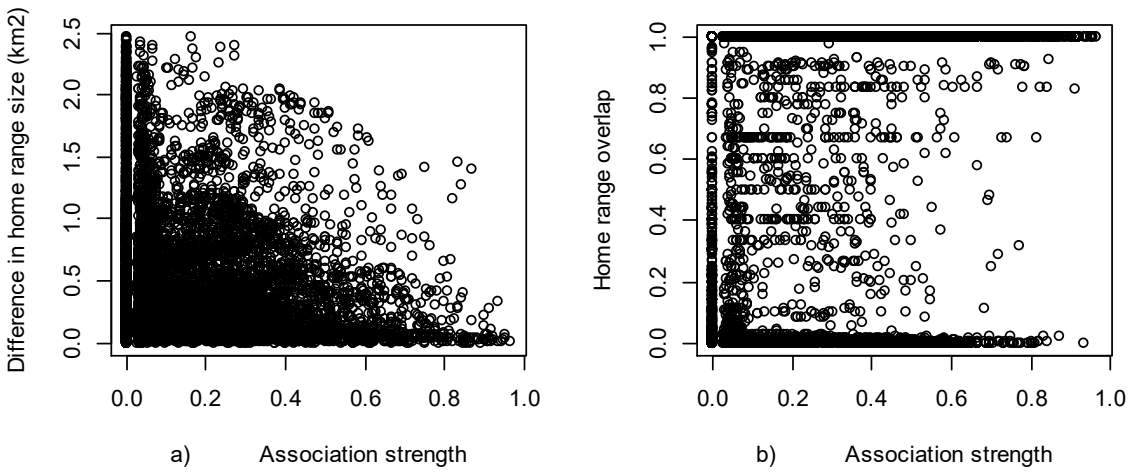


Figure 4.2. The relationship between association strength and a) home range size (in km^2) and b) home range overlap. Here, home range size difference values of 0 indicate that dyads used ranges that were the same size. Birds that were more strongly connected (higher association strengths) showed smaller differences in home range area (a) without, necessarily, using the same geographic area (b).

Simulated networks

The simulated networks - created by ranking strengths of associations and aggregating individuals at biologically relevant levels - found variation in movement levels between clusters to be higher than variation within clusters. Birds in the same ‘pair’ or ‘family’ in the simulated networks showed smaller differences in their home range area and site-hopping levels than birds from different families. As predicted, intra-cluster differences were smaller at the pair and family level than at the large flock and population level (Figure 4.3). Mean association strengths decreased as group level and number of group members increased (Table 4.4). Inter-cluster variation, the variation seen between social groups, was similar at all simulated levels of social structure (Figure 4.3).

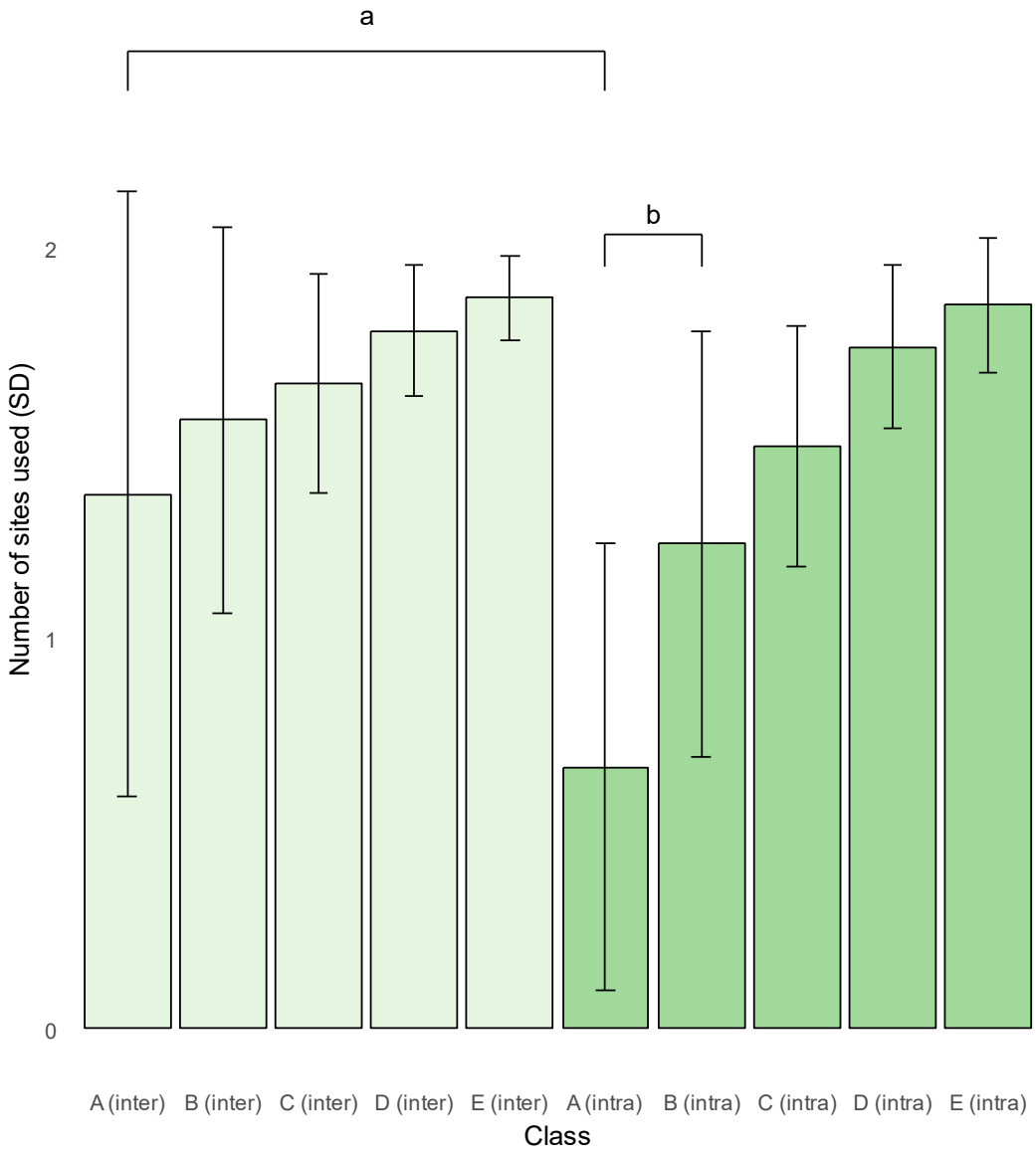


Figure 4.3. Intra- and inter-cluster variation in number of sites used for clusters of birds at the pair (A), family (B), small flock (C), large flock (D) and population (E) level. Similar patterns appear for home range area. a) The difference in variation between all pairs versus within all pairs, indicating homophily. b) The difference in variation within all pairs versus that within all families. Error bars indicate ±1SD. The variation seen between clusters at each social scale is shown in pale green and the variation seen within clusters at each social scale in dark green,

Table 4.4. Association strengths for each level of social group created in the ranked networks.

	Min.	1st Qu.	Median	Mean	3rd Qu.	Max.
Pair	0.356	0.758	0.821	0.805	0.898	0.964
Family	0.275	0.550	0.651	0.635	0.731	0.936
Small flock	0.050	0.357	0.432	0.439	0.527	0.739
Large flock	0	0.091	0.214	0.213	0.300	0.625
Population	0	0	0	0.019	0.031	0.250

Permutation linear mixed models found that individuals were more similar to those in their social cluster than to birds from other clusters at fine social scales (i.e. birds showed homophily to their pair and family) (Table 4.5). Homophily was not observed at larger social scales (in small or large flocks, with 16 and 60 members respectively). This suggests that association strength is a good predictor of movement levels at fine social scales.

Table 4.5. Output of permutation models looking at the correlation of intra- and inter-cluster variation (type) and cluster level (pair, family, small flock, large flock, population) with variation in the standard deviation of home range area and sites used in the ranked simulated networks.

Dependent variable	Predictor	Likelihood (LRT)	p
20% core home range area	Type	203.604	<0.01
	Level	26.385	0.257
	Type*Level	**184.075**	**<0.01**
Number of sites used	Type	273.347	<0.01
	Level	27.181	0.307
	Type*Level	**283.310**	**<0.01**

Group-level phenotype

Social groups, defined by the walktrap algorithm, did not differ in body condition in 2012 ($F_{4, 139}$=1.639, p=0.1678). However, in 2013, social groups differed in body condition with two groups losing body condition relative to the median and two gaining condition (Figure 4.4). This indicates that, although birds do not appear to assort by condition (they were no more similar in condition to their social group than the population in 2012), their social group was an important predictor of their condition in moult 2013 ($F_{4, 67}$=14.11, p<0.001). Three social groups (groups 3, 4 and 5) showed changes in body condition that differed significantly from zero (Table 4.6). Again, group ID was an important predictor of the change seen in body condition between years ($F_{4, 67}$= 8.476, p<0.001), with groups both decreasing and improving in condition between years (Figure 4.4).

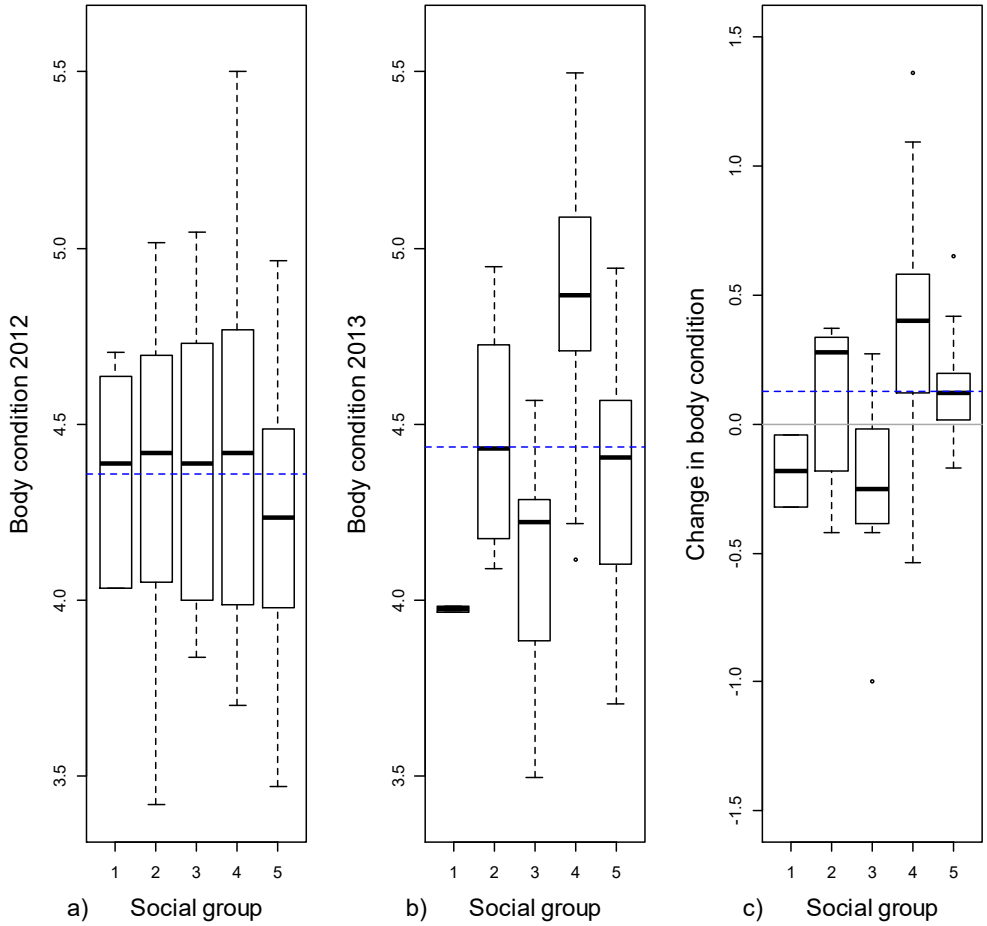


Figure 4.4. The relationship between body condition (scaled mass index) and social group in a) 2012, b) 2013 and c) Δ body condition. Dashed blue lines indicate the population median. The solid grey line (5c) indicates no change in body condition between years. In a), outliers at 2.193 (group 1) and 6.785 (group 3) not shown.

Table 4.6. Change in body condition over time: coefficients of model estimating the deviation of body condition from zero (no change in body condition relative to the population between years) for each of the five social groups.

Social group	Estimate	SE	t value	p
1	-0.182	0.221	-0.823	0.413
2	0.085	0.094	0.904	0.369
3	**-0.237**	**0.099**	**-2.391**	**0.020**
4	**0.422**	**0.068**	**6.167**	**<0.001**
5	**0.127**	**0.059**	**2.141**	**0.036**

Different social groups showed considerable variation in their movement behaviour in 2012-13. Group 2 and group 5 used comparable numbers of sites within the study area, but had vastly differing home ranges (Figure 4.5). Social group was an important predictor of movement at both fine (number of sites used: $F_{4, 140}=11.63$, $p<0.001$) and landscape (home range, 95% UD: $F_{4, 140}=13.12$, $p<0.001$) scales.

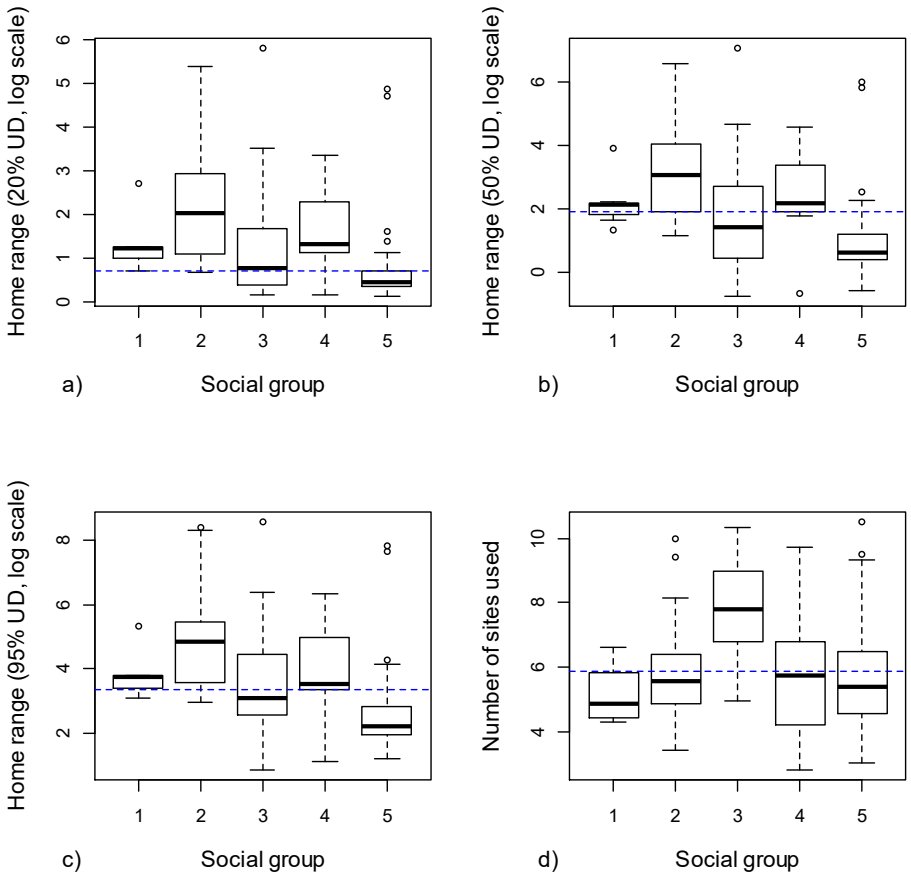


Figure 4.5. The relationship between movement and social group. Landscape-level movement is measured in home range area (km^2, log scale) at three levels of utilisation distribution: a) 20%, b) 50% and c) 95%. Fine-scale movement is shown as d) the number of sites used within the study area (corrected for number of observations). Dashed blue lines indicate the population median.

4.5 Discussion

This analysis of homophily within social groups and between strongly connected birds has established that, in line with our predictions, Canada geese are more similar in movement to the birds with which they associate frequently and different social groups display distinct phenotypes in their movement patterns and condition. Strong biological relationships, such as those between breeding pairs, are detectable in social networks. The high association strength seen between breeding pairs correlates with strong homophily in home range area and site use; birds were more similar to their mate than to other birds in their social group or the wider population. There is evidence to support assortative mating in this species with pairs showing similar body condition in the summer preceding breeding. Birds in the same 'pair' or 'family' in the simulated networks showed smaller differences in their home range area and site hopping levels than birds from different families. These geese do not appear to assort by condition (they were no more similar in condition to their social group than the population in 2012). However, their social group was an important predictor of their condition during moult in 2013, and of movement at both fine and landscape scales. Birds from social groups with larger ranges ended the year in better condition than birds from groups from smaller ranges. Overall, association strength predicts similarity in movement and condition at fine social scales, but groups vary unpredictably in their behaviour.

Breeding pairs were found to associate strongly in winter, as was expected in this species. The pair bond was recognisable within the winter network, with paired birds showing much stronger connections to their mate than those to other birds within their social cluster. This strong, year-round bond corresponded to strong homophily in movement propensity and range area and suggests that, in movement and network terms, breeding pairs are not independent. Pairs' co-dependence suggests that projects interested in establishing contact rates or contact network structure may only need to tag one of each breeding pair to

maximise the data acquisition (Newman et al. 2009). It may even support simplification in network or disease modelling by allowing pairs or small groups to be modelled as a single node. Indeed, the homophily observed in the movement behaviour of birds even up to the small flock level in the artificial network clusters may be helpful in projects looking at movement patterns. It suggests that closely studying a few birds from as many social groups as possible and extrapolating those birds' attributes to their close associates may yield more information about the system than closely studying all individuals from a small number of social groups.

The homophily in body condition observed in 2013 (but not 2012) suggests that in this system 'homophily' is passive rather than active. Homophily and assortment tend to imply active choice by the individuals involved, e.g. that individuals choose to join groups in which they will not stand out (Rodgers et al. 2011). However, many traits are plastic and physiological characteristics are determined by the individual's recent conditions. In this way, groups may develop similar characteristics, moving from their relative positions towards the group mean. The repeated measures of body condition suggest that these birds do not actively assort based on body condition but that individuals end the year in similar condition to their social group. This is consistent with passive homophily: homophily as a consequence of group membership. Group membership brings both benefits in terms of discovering resources (Aplin et al. 2012), which is likely to be evenly distributed across the group, and the possibility of increased competition for resources (Bijleveld et al. 2012), which is unlikely to be evenly distributed across the group.

The homophily in body condition seen within social groups in 2013 also supports the hypothesis that condition is a function of the resources available to that social group rather than of dominance hierarchy within the social group. This is reinforced by the evidence that it was the social groups with the larger home

ranges to finish the year of study in better condition. In geese, families are known to be dominant over pairs, which are dominant over single birds (Poisbleau et al. 2006). Since every social group would contain multiple families, pairs and single birds, the logical conclusion of a strong linear dominance hierarchy is heterophily in body condition within social groups, with the least dominant in poorest condition. However, social groups were homophilous with regard to body condition in 2013 (and change in body condition in years) and the variation seen in the population largely was due to differences seen between social groups.

The five social groups identified in this system showed individual combinations of movement propensity, range and condition that suggest that the effect of disease entering each group may be quite different. Change in body condition showed a longitudinal cline: groups in the west of the study area lost condition, and groups on the east of the study area gained condition. The groups at either extreme of the study site showed the largest changes in body condition in each direction. Social group 3 used a large number of sites (moving frequently around several separate lakes forming a lake complex) over an intermediate home range area, whilst two social groups (2 and 5) were found in the same geographic area, and did not differ in movement propensity, but differed greatly in their home range area. It may be that groups using more sites would be more likely to be exposed to infection; in this case the social group using more sites was also that which showed a decline in condition, potentially reducing individuals' ability to mount an effective immune response. These results support the hypothesis that the amount and type of movement can be a characteristic of the social group, and that movement needs to be understood at multiple scales to have a full picture of population movement.

Homophily was observed to be strongest in frequently associating birds and, in the artificial biological groups, at the 'pair', 'family' and 'small flock' levels. Somewhere between group sizes of 16 (small flock) and 35 (large flock, also the

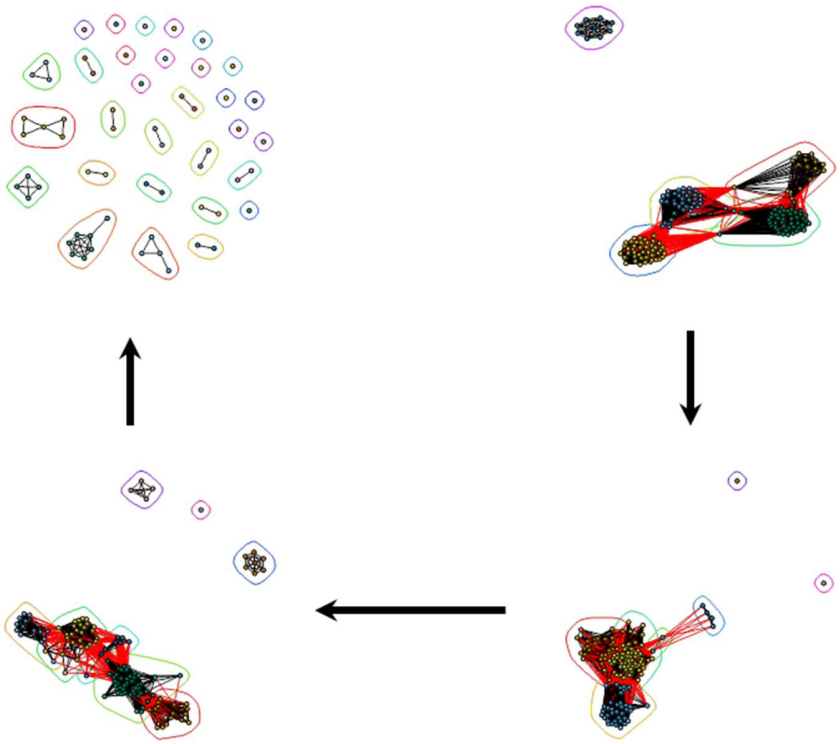
mean size of moult flocks in the study period) homophily declines. This suggests that either the ability or need to assort by phenotypic characteristics declines or the association frequency is not high enough to result in homophily. This absence of homophily may reflect the intimacy of the relationship. At the 'family' and 'small flock' levels, associations may be more meaningful whereas, at the 'large flock' level, birds coincide but interact less intimately. For example, in a large flock birds would be deemed interacting based on gambit of the group (Whitehead and Dufault 1999). However, being from different social groups they may never approach each other, as would be necessary for selection for homophily (e.g. for selection via the oddity effect (Rodgers et al. 2011)).

This functional independence, despite individuals' coincidence, is important when considering the transmission of different diseases. Highly-transmissible *E. coli* may be transmitted simply by sharing a site (Vanderwaal et al. 2013), whereas an agent requiring repeated exposure or transmission at close range (e.g. Tasmanian devil facial tumour disease (Hamede et al. 2013)) is unlikely to be transmitted by coincidence. Future disease models may be improved by including not only contact rates but also lagged contacts to represent individuals that are infected as a result of environmental transmission from a shared resource. For example, contact rates estimate the risk of disease transmission between birds that are observed in the same place at the same time. Lagged contact rates would estimate the risk of transmission for birds that use sites previously used by infected individuals within a certain time window, defined by the pathogen's ability to persist in the environment. Future research is needed to combine social network information with observed transmission networks, as has been done in studies of the Sin Nombre virus (Clay et al. 2009) and *Escherichia coli* (Vanderwaal et al. 2013), for economically important diseases.

There are several simple reasons why frequently associating should correlate with, and lead to, similarities in body condition, movement behaviour and myriad

biological variables. However, too often social networks are made and described without any context being given as to the biological differences between different social groups (Farine et al. 2015c). Clearly, different groups have distinct phenotypes and differ greatly in their movement propensities and home ranges: there were some small groups (‘families’) that used, over the year, twice as many sites as other groups. Given the potential in some traits for ‘social amplification’ to increase differences between groups (Canonge et al. 2011; Planas-Sitja I, Deneubourg J-L, Gibon C 2015), the differences seen in this snapshot of the wider social network would be worth further investigation. Additionally, in humans, when network structure is challenged, individuals preferentially retain their homophilous connections (McPherson et al. 2001). This suggests that when networks are perturbed, there may be some predictability in how they change. These findings suggest not all groups are of equivalent importance in disease transmission. Ideally, disease managers may consider not only the place of the group in the social network but also its phenotype in planning interventions. This study demonstrates the role that social network techniques can take. By placing individual variation in its proper social context, social network analysis also highlights the impact on population-level processes of what can be identified by these methods as not individual but group-level characteristics.

5. Seasonality in movement and contact rates and the implications for disease transmission.



5.1 Abstract

Disease peaks are strongly seasonal. So too are organisms, with years divided into phases of breeding, migration and growth. However, the precise patterns of seasonality in movement and contact rates have not been directly compared. Beta, the parameter quantifying transmission in disease models, is the outcome of several mechanisms, including movement and contact rates, and is therefore likely to vary seasonally. Here, transmission is simulated in seasonal contact and movement networks constructed from two complementary datasets of Canada goose (*Branta canadensis*) resightings. Transmission was fastest in movement networks in autumn (twice that of other seasons). More sites were infected in winter; however, simulated disease outbreaks covered the greatest area in autumn. Infections rarely led to even small outbreaks in spring, though most infections triggered outbreaks in summer, autumn and winter. In association networks reflecting contact rates, transmission was fastest in summer and winter (Cotswold short-term dataset) and summer and autumn (Thames long-term dataset). Contact networks were extremely dense and most birds were infected in fewer than five timesteps in summer, autumn and winter in both datasets. Combining contact and movement networks, it seems likely that an infectious agent will spread most swiftly and widely in autumn. Whilst disease peaks are strongly seasonal, disease outbreaks may strike at any time when moving between species; understanding the potential of both movement patterns and contact rates to transmit infection is key to understanding the disease' epidemiology.

5.2 Introduction

We live in a seasonal world. Seasonality, the occurrence of regular and predictable changes in environmental conditions, affects resource availability (Baden et al. 2016), habitat use (Havarua et al. 2014), movement (Loveridge and Macdonald 2001) and behaviour (Hamede et al. 2009). Heterogeneity in movement and contact behaviour is increasingly recognised to affect the transmission of disease (Lloyd-Smith et al. 2005; Ferrari et al. 2011); yet we lack a detailed understanding of how individual contact patterns change seasonally. A better understanding of how seasonal prevalence and seasonal contact patterns covary is crucial to developing effective disease management strategies (Altizer et al. 2006; Fisman 2007; Lachish et al. 2009; Tompkins et al. 2011), especially given the highly seasonal nature of epidemics (Wang et al. 2015). In this chapter I quantify seasonal contact rates in social birds with a view to understanding the influence of contact rate and movement patterns on disease transmission. I use social network analysis, which quantifies the contacts within a population, as a tool to assess seasonal variation in the social network and infer disease transmission (Wylie et al. 2005; Grear et al. 2013; Craft 2015).

Langwig et al. (2015) identify five ways in which seasonality may influence disease transmission: changes in habitat use (Loveridge and Macdonald 2001; Havarua et al. 2014; Baden et al. 2016), contact rates (Hollmén et al. 2003; Ji et al. 2005; Hamede et al. 2009), persistence of the agent within the environment (Nallar et al. 2015; Pitzer et al. 2015; Langwig et al. 2015; Penczykowski et al. 2015), ability to mount an immune response (Kortet et al. 2003; Mougeot et al. 2004; Hawley and Altizer 2011) and the presence of seasonal birth pulses (Hosseini et al. 2004; Wells et al. 2015). The difficulty comes in assessing the cumulative impact of all of these mechanisms, which may have complex interactions. For example, every year brings a newly-hatched, newly-emerged or new-born set of naïve hosts (a seasonal birth pulse). These pulses can trigger disease outbreaks (Hosseini et al. 2004; Duke-Sylvester et al. 2011; Van Dijk et al. 2014; Hayman 2015). The exact timing of the pulse can dictate the size of the

outbreak, not only in that year (Smith et al. 2009; Wang et al. 2015) but also the next (Smith et al. 2009). However, species with altricial young born in solitary dens or nests will be dissociated from their wider social group during rearing (Kinnaird and O'Brien 1999). This low level of contact may reduce their exposure to infection from conspecifics or via fomites. Seasonality of social behaviour and immunocompetence are also linked. For many species, contacts seem to increase around the breeding season (Hamede et al. 2009; Zohdy et al. 2012) and when resources are limited (e.g. during winter) (Hosseini et al. 2004; Böhm et al. 2008). Thus, contact rate increases at a time when animals may be experiencing immunosuppression by high androgen levels (Nolan et al. 1998; Peters 2000; Hughes and Randolph 2001b; Hughes and Randolph 2001a), high physiological costs (Zuk and Johnsen 1998; Kortet et al. 2003) or resource restriction (Hosseini et al. 2004). Knowing the cumulative impact of these five inputs to disease transmission can inform management (Beeton and McCallum 2011; Duke-Sylvester et al. 2011; Langwig et al. 2015). Yet, perhaps indicating the complexity of the relationships, there are few detailed empirical data on how prevalence, contact rates and movement levels covary seasonally.

Birds do it (Berthold et al. 2013), bees do it (Schneider and McNally 1992), many animals show seasonal changes in space use as a result of resource availability and environmental conditions. Long-distance movements in migratory species offer ample opportunities for exposure to different pathogens (Figuerola and Green 2000; Waldenström et al. 2002). Non-migratory species too show seasonal changes in space use with regard to their home range (Gehrt and Fritzell 1998; Malecki et al. 2001; Loveridge and Macdonald 2001; Campbell et al. 2013; Baden et al. 2016). Seasonal changes in habitat use (e.g. aggregation at hibernacula (Langwig et al. 2015)) may include altering not only the geographic location of habitat used but also the type of habitat used (Havarua et al. 2014). Whilst long-range movement, with its physiological costs, may reduce disease levels by eliminating weak individuals (Altizer et al. 2011), short-range movement will have none of these costs. Movement levels have been seen to

increase during the breeding season (Oakwood 2002; Hamede et al. 2009), in response to seasonal resources (Loveridge and Macdonald 2001; Baden et al. 2016) and decrease in cold weather (Ikeda et al. 2016). If periods of increased movement coincide with disease peaks, disease may be transmitted more swiftly through the landscape or to sympatric species with seasonal overlaps in habitat use (Loveridge and Macdonald 2001; Newman et al. 2009; Ikeda et al. 2016). Movement rates and contact rates are likely to be correlated (Otterstatter and Thomson 2007; Hu et al. 2013), but this assumes no territorial behaviour (limiting contact rates even at high movement levels) and no changes in density.

Gross seasonal aggregation patterns are well known for many, if not most, social species. Contact levels in many species rise during the breeding season (Hamede et al. 2009), though they may remain high in species that rear their young in social or colonial environments. However, species from geese (Silk 2014) to cows (Gygax et al. 2010) are now known to maintain preferred associations with particular individuals. These preferential associations (Swain and Bishop-Hurley 2007; Welsh and Herzing 2008) may mean that true contact rates are lower than those predicted during seasonal aggregation, potentially negating any assumed increase in disease risk. Many factors stratify contact rates in apparently homogenous populations, with preferential associations based on age (Naug 2008; Farine et al. 2015b), relatedness (Hirsch et al. 2012), role (Naug 2008; Pinter-Wollman et al. 2011), sex (Stanton and Mann 2012) or a combination of these (Wey and Blumstein 2010). When predicting seasonal disease risk in wild populations, a detailed understanding of this heterogeneity in contact rate is essential to accurate modelling (Kretzschmar and Morris 1996; Lloyd-Smith et al. 2005; Cross et al. 2007; Otterstatter and Thomson 2007; Posny and Wang 2014) since it creates structure within the population. Altering movement levels may lead to increases in contact rates (Leu et al. 2016); however there is little evidence to guide hypotheses regarding the relationship between movement behaviour and contact rates.

Social network analysis has been used to quantify contact rates in species from eusocial Hymenoptera (Otterstatter and Thomson 2007; Blonder and Dornhaus 2011; Pinter-Wollman et al. 2011) to the emphatically antisocial Tasmanian devil (*Sarcophilus harrisii* (Hamede et al. 2009; Hamede et al. 2012)). In line with revealing the cryptic structure in networks (Lusseau et al. 2003; Lusseau and Newman 2004; Podgórski et al. 2014), social network analysis has demonstrated that animal social networks may resemble 'small world' networks (Craft et al. 2011). These wild 'small world' networks are characterised by dense clusters of nodes between which there are frequent interconnections, linked by less frequent inter-cluster connections (Watts and Strogatz 1998). These networks tend to have a small number of steps between any two nodes (the 'six degrees of separation' phenomenon, (McCallum 2009)) and disease may swiftly spread between clusters, but the proportion of individuals infected is lower than in random networks (Christley et al. 2005). The clustering seen in social networks is thought to provide a degree of protection from disease transmission, since there are few connections between clusters via which disease may pass from one social group to another. However, despite the highly seasonal nature of most animal aggregations, seasonal fluctuations in contact rate have seldom been quantified.

Naturally, in constructing networks for predicting disease transmission, the network link must be led by the pathogen in question (Perkins et al. 2009; Grear et al. 2013). For pathogens spreading by the faecal-oral route or highly mobile vectors, association networks (coincidence at a site within a defined time period (Franks et al. 2010)) may be more important in predicting transmission (Bull et al. 2012; Vanderwaal et al. 2013) than networks based on physical contacts (e.g. grooming (Romano et al. 2016)). For other well-studied wildlife disease systems such as tuberculosis (Jenkins et al. 2007; Jenkins et al. 2012), Tasmanian devil facial tumour disease (Hamede et al. 2013) and rabies (Pastoret and Brochier 1999; Reynolds et al. 2015), physical contact or close association is likely to be required. However, some pathogens are extremely resistant to UV radiation and

desiccation (e.g. avian influenza viruses, avian TB (*Mycobacterium avium i)* and the plague bacterium *Yersinia pseudotuberculosis* (Gavier-Widén et al. 2012)). *Amblyomma limbatum* ticks are capable of occupying the same nest site, year after year, feeding whenever it is reoccupied (Leu et al. 2010b). In these cases, even association networks may be too specific and geographic networks, in which movements connect sites to provide a detailed picture of habitat use, may be preferred (Leu et al. 2010b; Paull et al. 2012).

To explore the relationship between seasonality in infection peaks and seasonality in social network structure, we require a pathogen with seasonal peaks and a host species with seasonal variation in social structure. Outbreaks of H5N1 highly pathogenic avian influenza (HPAI) peak in whooper swans (*Cygnus cygnus*) in spring, and in poultry in winter (Newman et al. 2009). HPAI is a current and highly significant threat: a 2014/15 outbreak in the US was responsible for the destruction of 50 million poultry at the cost of nearly a billion US dollars (David 2016). In wild birds, low pathogenic avian influenza infection peaks in early autumn, with prevalence reaching 25% during aggregation before migration and prevalence declining to undetectable levels in winter (Gavier-Widén et al. 2012). Spring and breeding levels are low-intermediate (Gavier-Widén et al. 2012). HPAI virus has been found to remain infective in fresh water for over three months at 4^{o}C (Stallknecht et al. 1990; Brown et al. 2009) and cold weather seems to favour HPAI H5N1 virus transmission, though this may be the result of seasonal behaviour or viral persistence (Munster et al. 2007; Gavier-Widén et al. 2012). HPAI has been found to have a high reproduction ratio (with each case leading to a mean of 6.5 others in an H7N7 epidemic in the Netherlands (Stegeman et al. 2004)), meaning that it is capable of fast transmission, therefore effective knowledge of how best to manage disease spread is vital.

UK-resident Canada geese (*Branta canadensis)* show seasonal changes in aggregation whilst occupying the same geographic area year-round, allowing for

comparisons between contact rates and aggregation patterns to be made more readily than in migratory species. Birds are highly social for much of the year, forming stable moult flocks in summer, highly fluid flocks in autumn and large aggregations in winter. In the breeding season, breeding pairs defend territories whilst non-breeding birds forage in flocks. Each season (breeding, moult, post-moult, winter) is likely to have a distinct network structure, with many small, transmission-limiting clusters in the breeding season and transmission-facilitating mixing in the post-moult period. Low movement levels during breeding and moult seasons may also constrain transmission. Though birds aggregate in winter, their choice of sites is limited, meaning that movement levels may be low, potentially constraining transmission. Canada geese are subject to seasonal outbreaks of *Escherichia coli* (Middleton and Ambrose 2005), *Helicobacter spp.* (Fox et al. 2000; Fox et al. 2006), Cryptococcus (Filion et al. 2006) and avian influenza (Bonner et al. 2004; Pasick et al. 2007; Kistler et al. 2012). They also frequently share sites with migratory waterfowl, which may be important in the long-range transmission of disease (Gilbert et al. 2006; Global Consortium for H5N8 and Related Influenza Viruses 2016; Elmberg et al. 2017).

This chapter looks at how seasonal contact and movement rates interact in a wild bird population, and how these compare with seasonal peaks in avian influenza. Disease transmission is simulated through seasonal association networks (based on shared site use) and seasonal geographic networks (based on movements between sites) to reflect spread by aerosol, faecal-oral and environmental routes. Seasonality of global network structure is quantified by calculating the extent of clustering (modularity) and the number of steps needed to traverse the network (path length). Epidemic spread is simulated in each seasonal network to estimate the potential impact of seasonality on the time between infection and outbreak. If fracturing of the network in spring into breeding pairs constrains disease transmission, as predicted, both the proportion of individuals infected and the speed of transmission will be lower in spring networks. In addition if, in the absence of any social preferences or territoriality, seasonal contact rates and

seasonal movement covary then transmission will peak in the same seasons. By linking the timing of infection peaks and the seasonality of network structure, this chapter aims to bridge the gap in our understanding of how the network structure at the point at which infection enters a population may affect the size and extent of the outbreak.

5.3 Methods

Datasets

Two datasets were used in these analyses: i) Cotswold dataset, containing observations from July 2012 to June 2014 of 188 marked Canada geese caught in the moult at the Cotswold Water Park, UK; and ii) Thames dataset, containing observations from 1st November 2000 to 31st October 2005 of 4212 marked Canada geese caught in the moult at sites along the River Thames, UK.

Study systems

Canada geese were first introduced to the UK in the 17th century. There are estimated to be 62,000 breeding pairs of UK-resident Canada geese and an estimated wintering population of 190,000 individuals (Musgrove et al. 2013). UK-resident Canada geese form flocks consisting of 3-400+ birds depending on season and region. During the breeding season (March-June), breeding pairs split off and defend territories, whilst non-breeding birds remain in flocks. Canada geese moult their flight feathers, annually timed to follow breeding. During the moult, breeding pairs, offspring and non-breeders congregate together in moulting flocks. This flightless period extends from June into July, when entire flocks can be caught.

The study area within the Cotswold Water Park, UK, (Ordnance Survey grid reference SU 0796) is an area of working and restored gravel pits covering 85km^2 near Cricklade, Wiltshire (OS grid reference SU 09857 93574). The 140 waterbodies are largely privately owned and managed, primarily for watersports and angling, but the Cotswold Water Park Trust oversees the area (which includes land in Wiltshire, Gloucestershire and Oxfordshire) and has the role of recording and advising on biodiversity and wildfowl management within the park. The lakes are surrounded by farmland, nature reserves, holiday accommodation and small settlements. Canada geese are resident at this site all year round with a wintering population in excess of 600 breeding pairs (Holt et al. 2015). The combination of numerous water bodies bordered by amenity grassland and

arable fields provides much suitable habitat for this species and the main methods of population control are planned management by shooting and egg oiling. In July 2012 and 2013, geese were rounded up and marked under licence by an experienced team. Adult birds were fitted with highly visible neck collars bearing unique codes and adults and juveniles with metal British Trust for Ornithology (BTO) leg rings in accordance with local ringing practices. Neck collars (dimensions: inner diameter = 42mm, height = 65mm) were produced by Interrex and were formed of black plastic overlaid with orange, so that the two-letter codes appeared as black text on an orange background.

The study area in the Thames dataset extends along the lower portion of the River Thames and the lakes to the west of London, resightings within OS grid squares TQ and SU (Figure 1). This area comprises amenity grassland, farmland and reservoirs frequently used by the geese. A long-term study marked 5768 geese between 1991 and the early 2000s with coded leg rings bearing a three digit alpha or alphanumeric code and metal BTO leg rings. Birds were resighted 1991-2012, with a high number of resightings in the period 2000-2005.

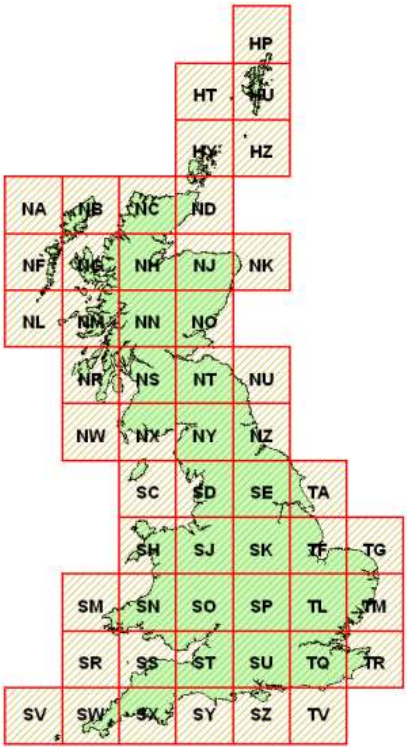


Figure 5.1. Map of Great Britain showing OS grid reference squares. Resightings of the Thames birds were from within squares TQ and SU, resightings of Cotswold birds were from within squares ST, SU and SP. Picture credit: Digimap, Edina.

Construction of the networks

Collar (Cotswold birds) and leg (Thames birds) codes of marked individuals were recorded in the field with binoculars and a telescope. Group membership, location, flock size, time and date were also recorded. Resightings took place in every month of the year and from dawn until dusk.

Birds in a flock present at the same site at the same time were judged to be associating in gambit of the group (Franks et al. 2010) and each of these group associations was termed an ‘event’. The extent of flock membership was determined by a chain rule based upon local geography and the distances between birds – birds were considered to be within a flock if they were in visual contact, were not separated by barriers such as hedges or by distances four

times greater than the mean inter-individual distance (measured in goose body-lengths to allow accurate calculation of distances at distance). On water bodies, all individuals present on the lake were assumed to be associating. In the field, groups of geese tended to stay away from field margins or boundaries and self-organised into cohesive flocks. All fission-fusion events were recorded, with small groups of individuals that arrived or departed separately from the main flock recorded both as part of the large flock and as a subunit in a separate 'event'.

A matrix of these co-occurrences was then used to calculate an index measuring strength of association between birds. The half-weight index is commonly used in social network analysis for the construction of social networks where nodes are more likely to be observed when not associated, or when not all individuals can be identified (Whitehead 2008). The half-weight index assigns each pair of individuals an association strength based upon the number of times they are seen together (x) versus separately in different periods (y_A+y_B) or separately in the same period (y_{AB}).

$$\text{Half-weight index} = x/(x+y_{AB}+1/2*(y_A+y_B))$$

In order to describe the passage of disease through goose populations in different seasons, seasonal association and movement networks were constructed from site use data in the Cotswold and Thames datasets. The year was split into four sections broadly reflecting goose seasonal behaviour: spring (March-May), containing the breeding season; summer (June and July), containing the moult; autumn (August-October), the post-moult period; and winter (November-February). The Cotswold dataset (2012-2013) yielded one network per season, whilst the Thames dataset (2000-2005) yielded five networks per season (Table 5.1), which varied in size (Table 5.2).

Table 5.1. Summary of seasonal networks.

Dataset	Type of network	Node – Edge	Season	Time period (number of networks)
Cotswold	Association, undirected	Individual – Shared site use	Spring	Mar-May 2013 (1)
			Summer	Jul 2012 (1)
			Autumn	Aug-Oct 2012 (1)
			Winter	Nov 2012-Feb 2013 (1)
	Movement, directed	Site – Number of birds moving	Spring	Mar-May 2013 (1)
			Summer	Jul 2012 (1)
			Autumn	Aug-Oct 2012 (1)
			Winter	Nov 2012-Feb 2013 (1)
Thames	Association, undirected	Individual – Shared site use	Spring	Mar-May (5)
			Summer	Jun-Jul (5)
			Autumn	Aug-Oct (5)
			Winter	Nov-Feb (5)

Table 5.2. Sizes of seasonal networks.

Network	Number of nodes in network			
	Spring	Summer	Autumn	Winter
Thames association network, 2001	45	1400	557	162
Thames association network, 2002	177	590	297	426
Thames association network, 2003	183	780	299	239
Thames association network, 2004	134	1496	412	160
Thames association network, 2005	110	251	131	416
Cotswold association network	58	153	125	142
Cotswold movement network	21	11	21	35

Calculation of social network metrics

Path length and modularity were calculated for each seasonal network. Path length captures both the density of the network and the distribution of the edges by quantifying how many steps are needed to cross the network (Croft et al. 2008; Whitehead 2008). Modularity is a measure of homogeneity, with low modularity seen in homogeneous networks and high modularity seen in networks with several distinct clusters or communities (Croft et al. 2008; Whitehead 2008). All network metrics were calculated in R (version 3.2.2, package igraph (Csardi and Tamas 2006)). Path length was calculated in two ways using the mean distance command: i) measuring the distance between connected nodes and ii) measuring the distance between all nodes (substituting the maximum path length where no possible path existed between nodes) divided by the size of the network. These two methods are complementary since the first captures spread through the main part of the network, and the second captures path length across the network incorporating isolates. Modularity of the weighted networks was calculated using the walktrap algorithm.

Epidemic spreading

Epidemic spreading was modelled in each seasonal network in a similar (though simpler) manner to Dybiec et al. 2004, adapting code written by Walker and Kleczkowski 2015 (Dybiec et al. 2004; Walker and Kleczkowski 2015). Epidemic spread was simulated by infecting a single node at random then looping through its connected nodes and infecting a sample of these with the probability, p. The infection process was repeated for newly infected nodes in the next time step. Infected nodes moved in each time step to non-infectious status (signifying death or recovery with immunity) with the probability q (Walker and Kleczkowski 2015). Each simulation ended at the first time step at which there were no infected nodes. A sensitivity analysis was run on the Cotswold association networks to establish the networks' sensitivity to variation in the infection and recovery parameters p and q.

Transmission rates in geese (and many other waterfowl) are unknown (Tiensin et al. 2007). However, in chickens, controlled transmission experiments found that 63.6% of birds kept in close contact with a bird inoculated with HPAI virus subsequently become infected (Bouma et al. 2009). Chickens tend to be more severely affected by HPAI than geese (Gavier-Widén et al. 2012), therefore this was taken as representative of the upper bounds of transmissibility and the infection probabilities (p) were set as 0.125, 0.25 and 0.5.

High, medium and low rates of q (probability of death) were set with reference to the literature. HPAI commonly causes death in poultry within days of infection, with infection in wild birds estimated to lead to death in 5-15 days (Stegeman et al. 2004; Hulse-Post et al. 2005; Bouma et al. 2009; Gavier-Widén et al. 2012; Pandit et al. 2013). Lower values of p (0.125) reflect agents that have lower infectivity or transmissibility, higher values (0.5) reflect highly infective agents (e.g. those requiring only a small amount of inoculum or infection window to infect). Low values of q (0.06) reflect asymptomatic individuals capable of shedding virus for an extended period (Hulse-Post et al. 2005; van der Goot et al. 2008) and high values of q (0.5) reflect birds that succumb to infection and recover (or die) within a matter of days (Pasick et al. 2007; Newman et al. 2009). Values of q and their equivalent infection duration are shown in Table 5.3.

Table 5.3. Values of q used in epidemic spread simulations and the equivalent infection duration for 90% of birds.

q	Infection duration (days)
0.06	15
0.2	5
0.35	3
0.5	2
0.9	1

Association networks (individuals as nodes connected by edges reflecting the number of times the dyad associated): The probability of infection was set as 0.125 and the probability of recovery at 0.35 with a single individual infected at the first time step. Movement networks (sites as nodes connected by edges reflecting the number of movements made between sites): The probability of infection was set as 0.1 and the probability of recovery at 0.5 with a single site infected at the first time step.

Transmission was simulated in each seasonal network of the Thames and Cotswold datasets 100 times. The state of each node at each time step (naïve, infected or recovered) was recorded. The number of time steps to saturation of the network or infection die-off (whichever occurred first) was then recorded, as well as the number of nodes newly infected, and those remaining infected at each time step. These measures capture the speed and extent to which an infectious agent penetrates the network and the protective capabilities of different network structures. The number and proportion of nodes infected, the outbreak duration, latency to each outbreak threshold and mean speed of transmission (proportion infection/outbreak duration) was calculated for each simulation. Outbreak thresholds were set from 5 to 50 birds, at intervals at 5 birds.

Statistical analysis

Transmission through seasonal association networks (Cotswold and Thames datasets) and movement networks (Cotswold dataset) was quantified using linear and generalised linear models run in R (version 3.3.1, package lme4 (Bates et al. 2015)). Transmission was measured in four ways:

a) the number of infections that resulted in outbreaks (setting the outbreak threshold at ten infections)
b) the latency for the infection to reach the outbreak threshold
c) the number of nodes infected during outbreaks
d) the mean speed of transmission across the network during outbreaks.

In each model, season was given as the main predictor variable, either alone or in combination with outbreak threshold level or year. Models are described in detail in Table 5.4.

Kolmogorov-Smirnov tests were used to test whether distributions of area of disease spread differed between seasons because of the highly non-normal data. These calculate the cumulative difference between two distributions and can compare distributions differing in both mean and variance (Wilcox 2005).

Table 5.4. Overview of analyses conducted upon datasets of simulated transmission through observed seasonal networks. Association networks (AN) and geographic movement networks (GN) were analysed using linear models (LM), generalised linear models (GLM), linear mixed models (LMM), generalised linear mixed models (GLMM) or pairwise Kolmogorov–Smirnov (KS) tests.

Model Structure	Dataset	Analysis	Random effect
Number of infections resulting in outbreaks ~ season + outbreak threshold	Cotswold AN	Quasibinomial GLM	NA
Number of infections resulting in outbreaks ~ season*outbreak threshold + season*year	Thames AN	Quasibinomial GLM	None
Timesteps between infection and outbreak ~ season * outbreak threshold	Cotswold AN	Quasibinomial GLM	NA
Timesteps between infection and outbreak (log^{10}) ~ season * outbreak threshold	Thames AN	Gaussian LMER, logged y	Year
Number infected (corrected for network size) ~ season	Cotswold AN	Quasibinomial GLM	NA
Number infected (corrected for network size) ~ season	Thames AN	Poisson GLMM	Year
Number infected (corrected for network size) ~ season	Cotswold GN	Gamma (log) GLM	NA
Mean transmission speed of outbreak ~ season	Cotswold AN	Gaussian LM	NA
Mean transmission speed of outbreak (log^{10}) ~ season	Thames AN	Gaussian LMM	Year
Mean transmission speed ~ season	Cotswold GN	Gamma (log) GLM	NA
Area of disease spread (distribution of season 1 ~ distribution of season 2)	Cotswold GN	Pairwise KS tests	NA

5.4 Results

Seasonal network structure

Both movement and association networks reveal high seasonality, with a very low level of clustering within the network (measured by modularity) in autumn, indicating that birds were mixing rather than segregating into distinct social groups. In spring and summer, social groups were more distinct within the association networks (Figure 5.2). Modularity was low in all seasons in the movement networks, indicating that birds moved frequently between several different sites rather than following particular routes or regularly cycling between the same few sites.

Path lengths between connected nodes were shortest in spring, suggesting fast transmission, and longest in autumn, suggesting slower transmission (Figure 5.3a). However, path lengths across the whole network, corrected for network size, were longest in spring and shortest in summer and autumn (Figure 5.3b). This indicates that spring networks are composed of many small groups of very closely connected birds, with few links between these groups. Though path lengths within these social groups may be short, the fractured pattern means that path lengths across the whole network are long. For example, during summer 2004 in the Thames dataset birds were resighted more frequently than in other years. This led to more associations between social groups being observed and fewer isolated social groups in the final network. The presence of these edges between social groups resulted in longer path lengths within the relatively large main component of the network and shorter path lengths across the network.

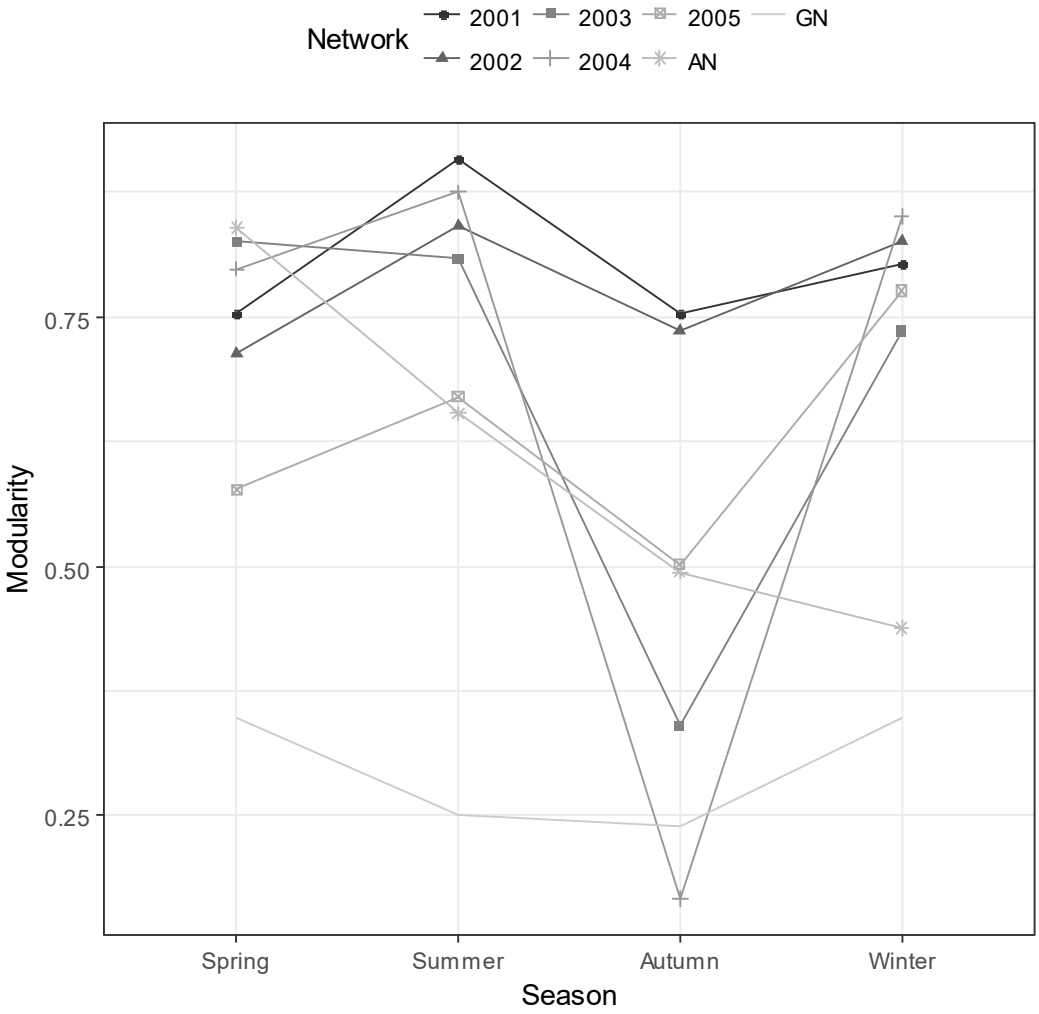


Figure 5.2. Modularity (of weighted networks), calculated using the walktrap algorithm showing fall in modularity in autumn.

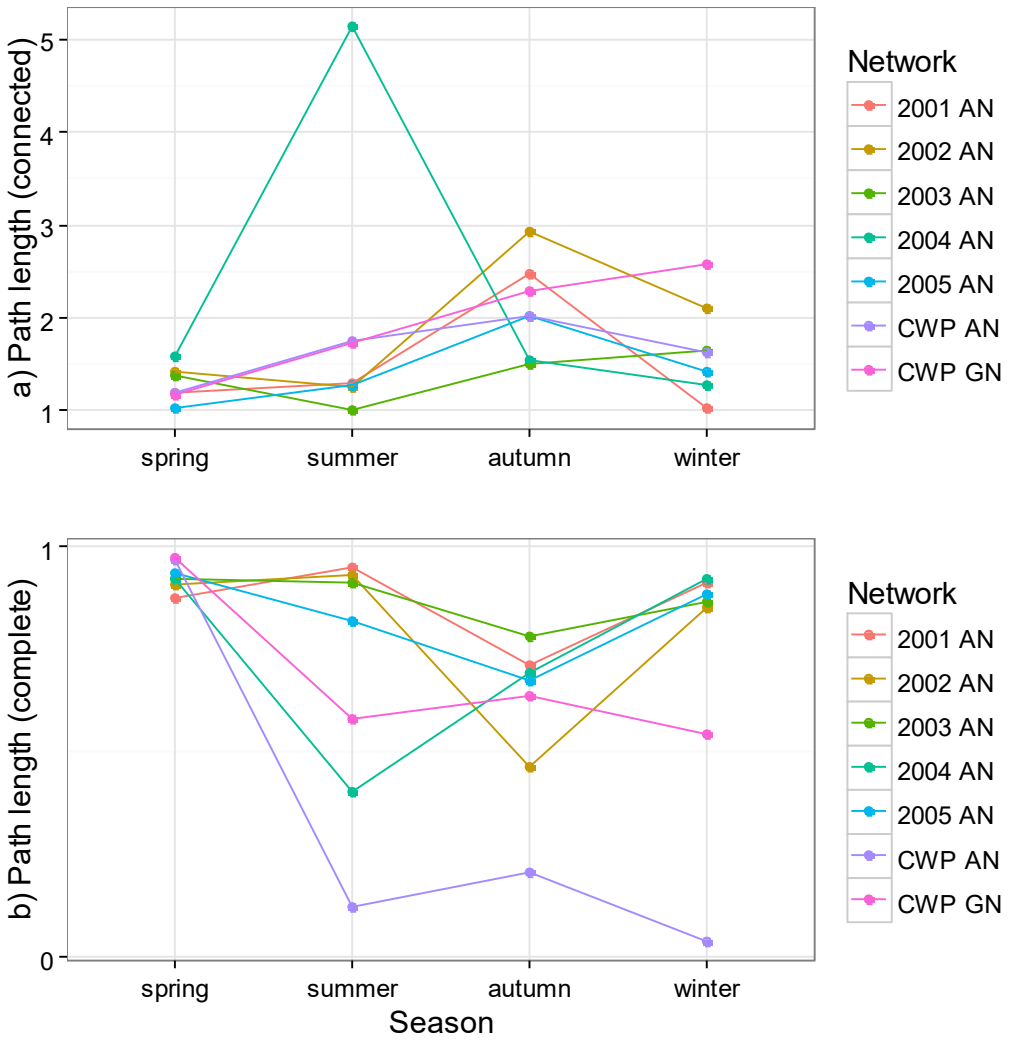


Figure 5.3. Path lengths in spring, summer, autumn and winter through association (AN) and movement (GN) networks. Shorter path lengths indicate networks in which transmission is faster. Path lengths are calculated for a) only nodes which are connected to each other; b) the entire network, corrected for network size.

Simulated networks

Overall, transmission varied greatly by season, with summer, autumn and winter association networks facilitating transmission and spring networks constraining transmission. Looking only at the Cotswold dataset, winter association networks

most facilitated transmission, with more outbreaks ($X^2_{3, 35}$=3251.7, p<0.001) in winter for each outbreak threshold level. When considering infections leading to outbreaks infecting at least ten birds (the outbreak threshold used throughout for statistical analysis), more birds were infected ($X^2_{2, 272}$=650.22, p<0.001) and transmission speeds were faster (adj r^2=0.344, $F_{2, 272}$=72.8, p<0.001, Table 5.5) in winter than in other seasons.

Table 5.5. Model coefficients predicting a) number of outbreaks, b) proportion of birds infected in outbreaks and c) mean speed of transmission by season in the Cotswold association networks. No infection led to an outbreak in spring networks.

	Season	Estimate	SE	t value	p
Number of outbreaks	Spring	NA	NA	NA	NA
	Summer	2.647	0.166	3.299	0.002
	Autumn	2.100	0.178	11.818	<0.001
	Winter	3.342	0.204	6.077	<0.001
	Outbreak level	-0.006	0.005	-1.150	0.258
Proportion of birds infected in outbreak	Summer	2.744	0.024	113.55	<0.001
	Autumn	2.087	0.031	-21.41	<0.001
	Winter	3.830	0.046	23.64	<0.001
Mean transmission speed	Summer	8.003	0.125	63.932	<0.001
	Autumn	6.252	0.180	-9.753	<0.001
	Winter	8.231	0.175	1.302	0.194

Looking only at the Thames dataset (for which there were five years' data rather than one), the pattern changed slightly from year to year (Figure 5.4); however, transmission was facilitated most in summer and autumn association networks. Infections were most likely to lead to outbreaks in summer association networks

($X^2_{18, 176}$=7572.7, p<0.001, Figure 5.4). However, the proportion of birds infected ($X^2_{2,5}$=6539.4, p<0.001, Figure 5.5) and the mean speed of transmission through the network were substantially higher in autumn than in summer ($X^2_{3, 6}$=427, p<0.001, Table 5.6, Figure 5.9).

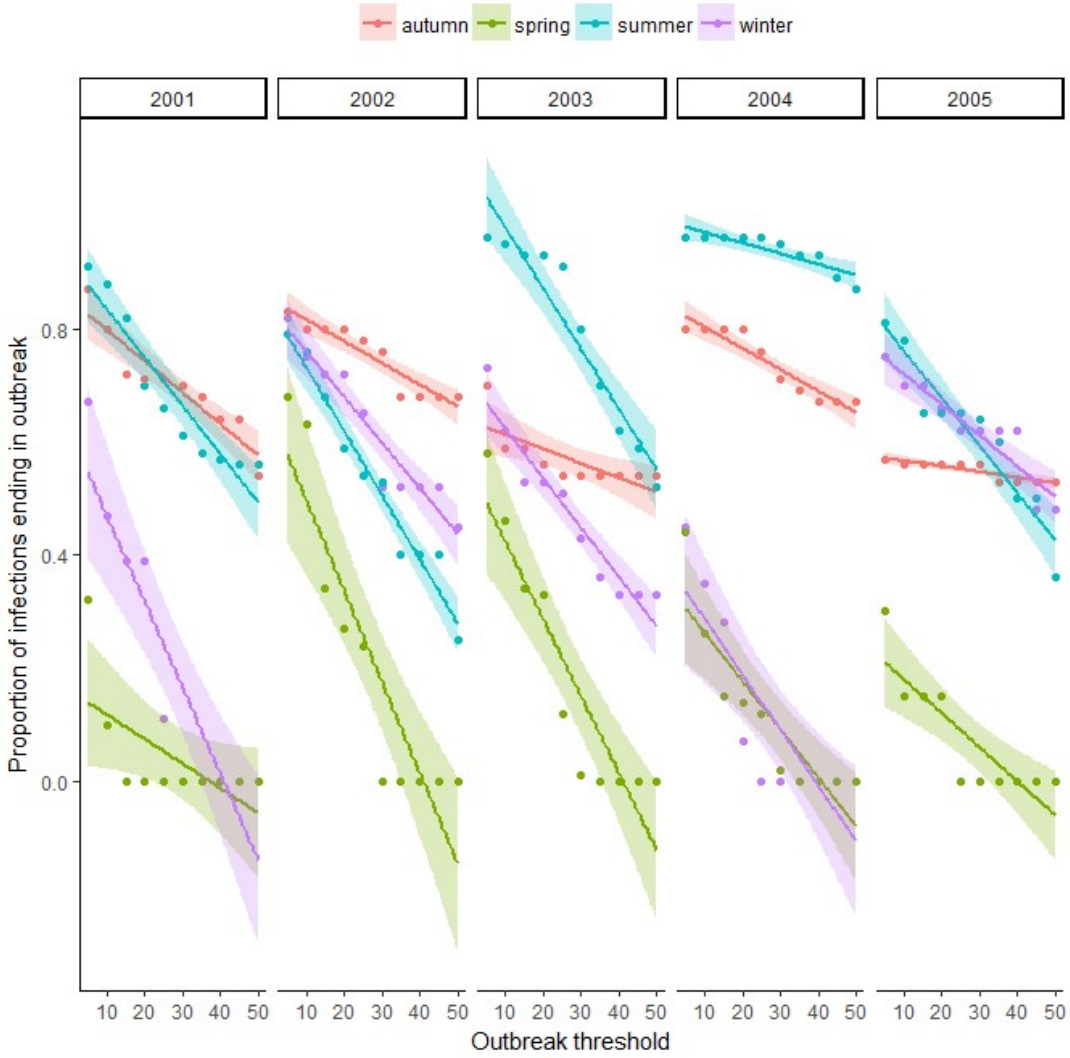


Figure 5.4. Proportion of infections triggering outbreaks in Thames seasonal association networks. Here outbreak threshold is the number of infections necessary for the simulation to be considered an outbreak.

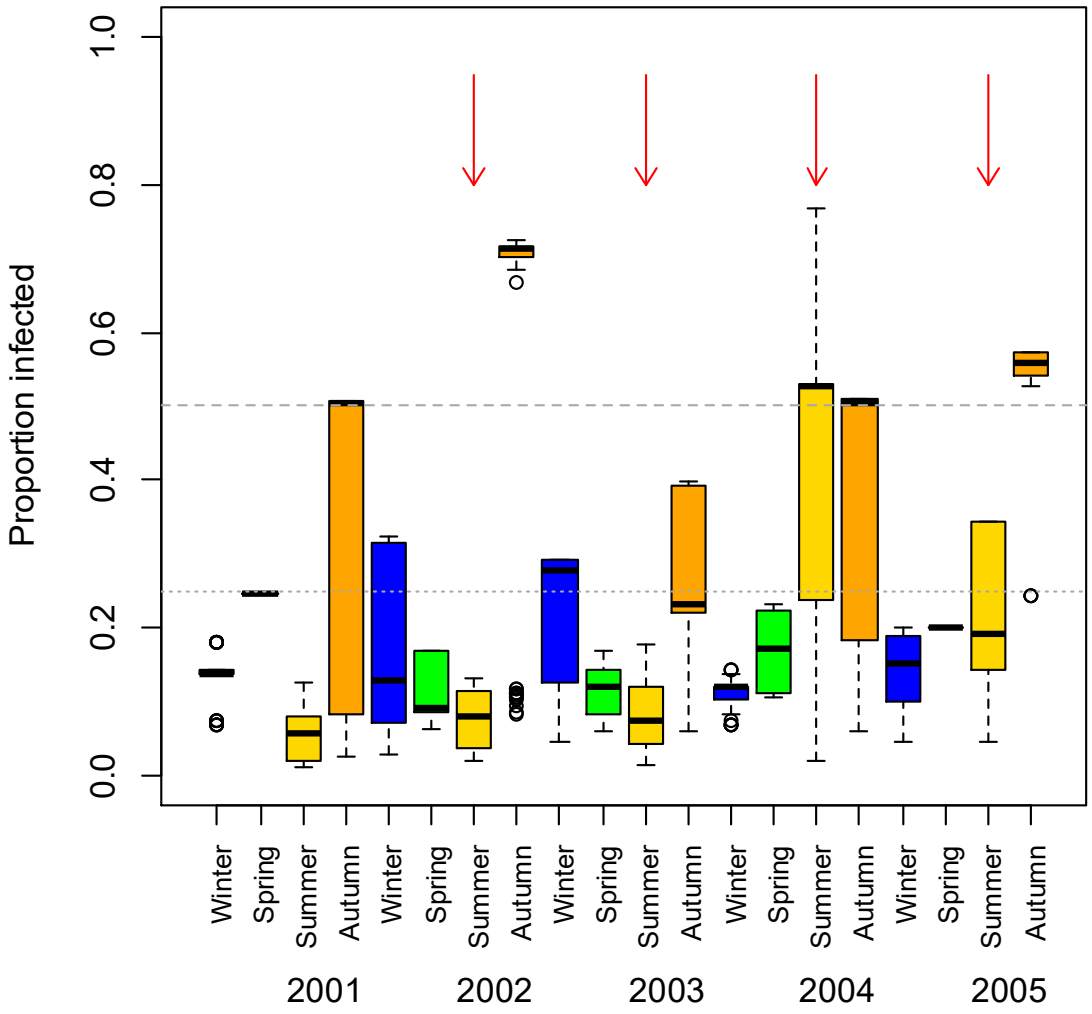


Figure 5.5. Boxplot showing median, interquartile range and extent of data for the proportion of birds infected in outbreaks in each season in seasonal association networks of Thames birds (outbreak threshold = ten birds infected). Red arrows indicate culling in that season. Grey dotted line indicates 25% of birds infected in an outbreak and the grey dashed line indicates 50% of birds infected in an outbreak.

Table 5.6. Model coefficients predicting a) proportion of birds infected in outbreaks and b) mean speed of transmission by season in the Thames association networks.

a)

	Estimate	SE	z value	p value
Spring	2.591	0.025	-5.23	<0.001
Summer	2.839	0.018	6.23	<0.001
Autumn	3.703	0.017	58.80	<0.001
Winter	2.724	0.123	22.22	<0.001

b)

	Estimate	SE	t value
Spring	2.409	1.058	-7.942
Summer	6.301	1.044	11.829
Autumn	6.911	1.046	13.375
Winter	3.766	1.120	11.672

In the networks of movement between sites in the Cotswold study area, transmission was fastest ($X^2_{3,290}$=989.66, p<0.001), proportion of sites infected highest ($X^2_{3,290}$=110.11, p<0.001) and area of spread greatest (Figure 5.6) in autumn (Table 5.7). Paired Kolmogorov-Smirnov tests identified that the greatest differences in area of disease extent were found between spring/summer and winter outbreaks (Table 5.7b).

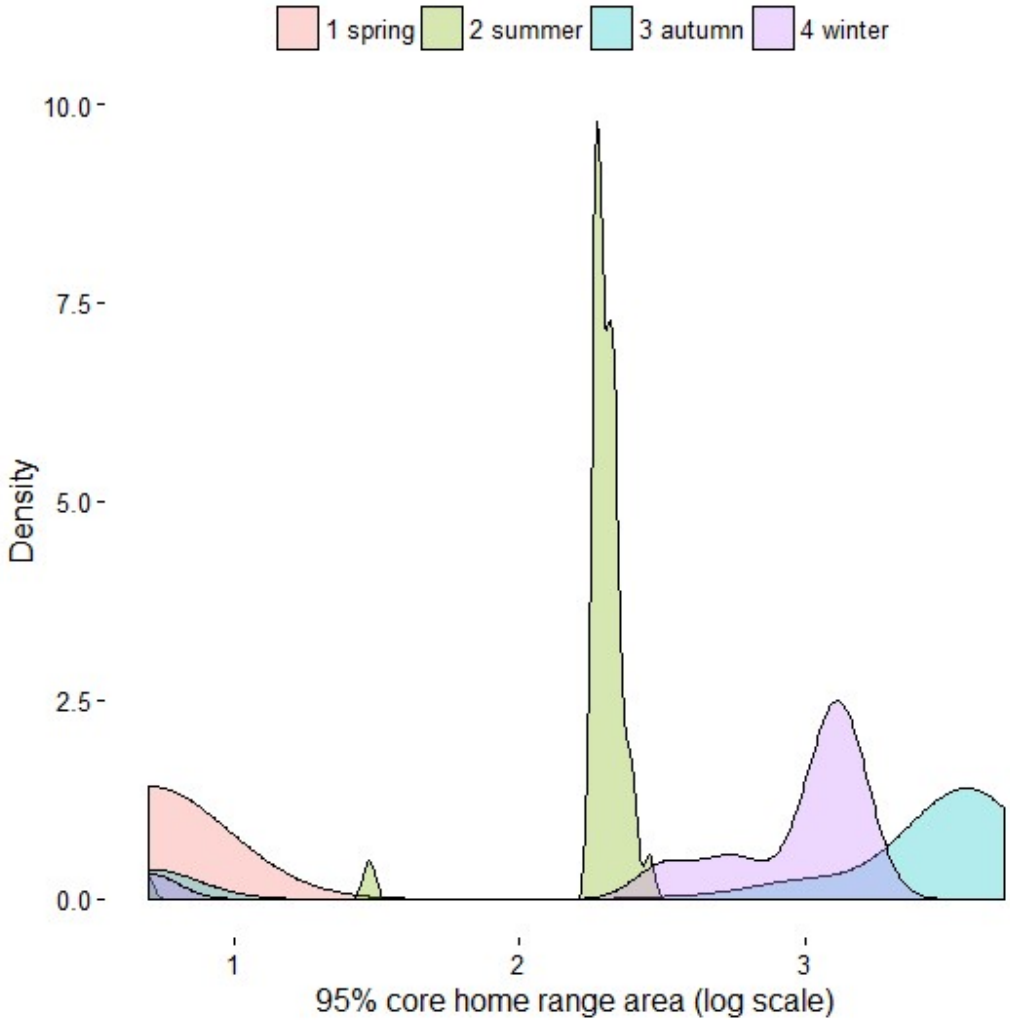


Figure 5.6. Density plot showing magnitude of disease spread in each season in the Cotswold movement network in km^2. All disease outbreaks in spring affected a very small area (<10km^2), whilst in summer, most disease outbreaks covered 200-300km^2. Density plots are similar to a smoothed histogram.

Table 5.7. Model coefficients predicting a) proportion of sites infected and mean speed of transmission and b) differences in area of disease transmission by season in the Cotswold movement networks (all $p<0.001$), calculated by pairwise Kolmogorov-Smirnov tests.

a)

	Season	Estimate	SE	t value	p value
Proportion of sites infected	Spring	2.455	0.036	68.43	<0.001
	Summer	4.419	0.047	41.88	<0.001
	Autumn	4.237	0.048	37.37	<0.001
	Winter	4.384	0.046	41.84	<0.001
Mean transmission speed *(infections per day)*	Spring	-1.751	0.204	-8.571	<0.001
	Summer	2.388	0.267	15.496	<0.001
	Autumn	5.287	0.272	25.907	<0.001
	Winter	2.429	0.263	15.920	<0.001

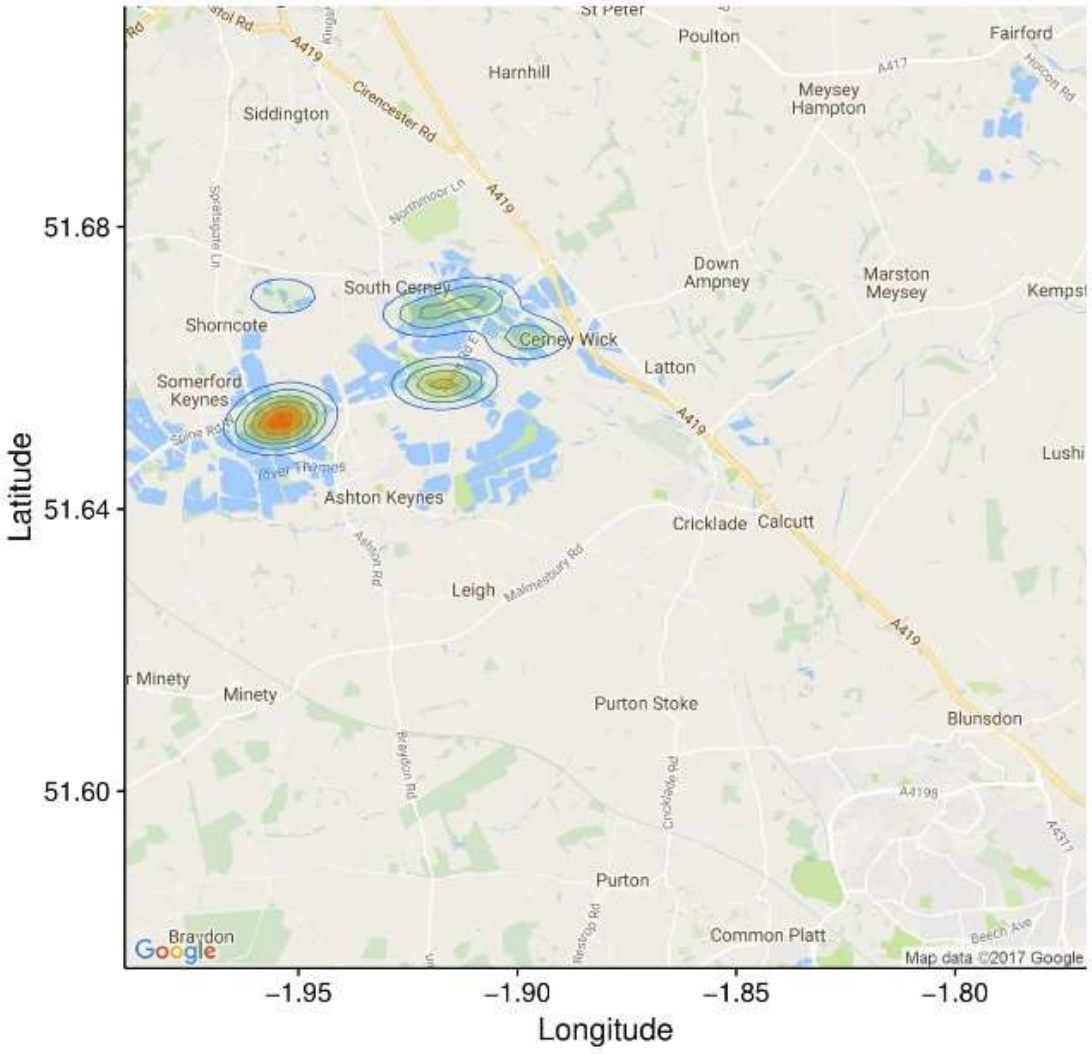
b)

	Summer	Autumn	Winter
Spring	**0.987**	**0.836**	**0.919**
Summer	-	**0.836**	**0.919**
Autumn	-	-	**0.726**

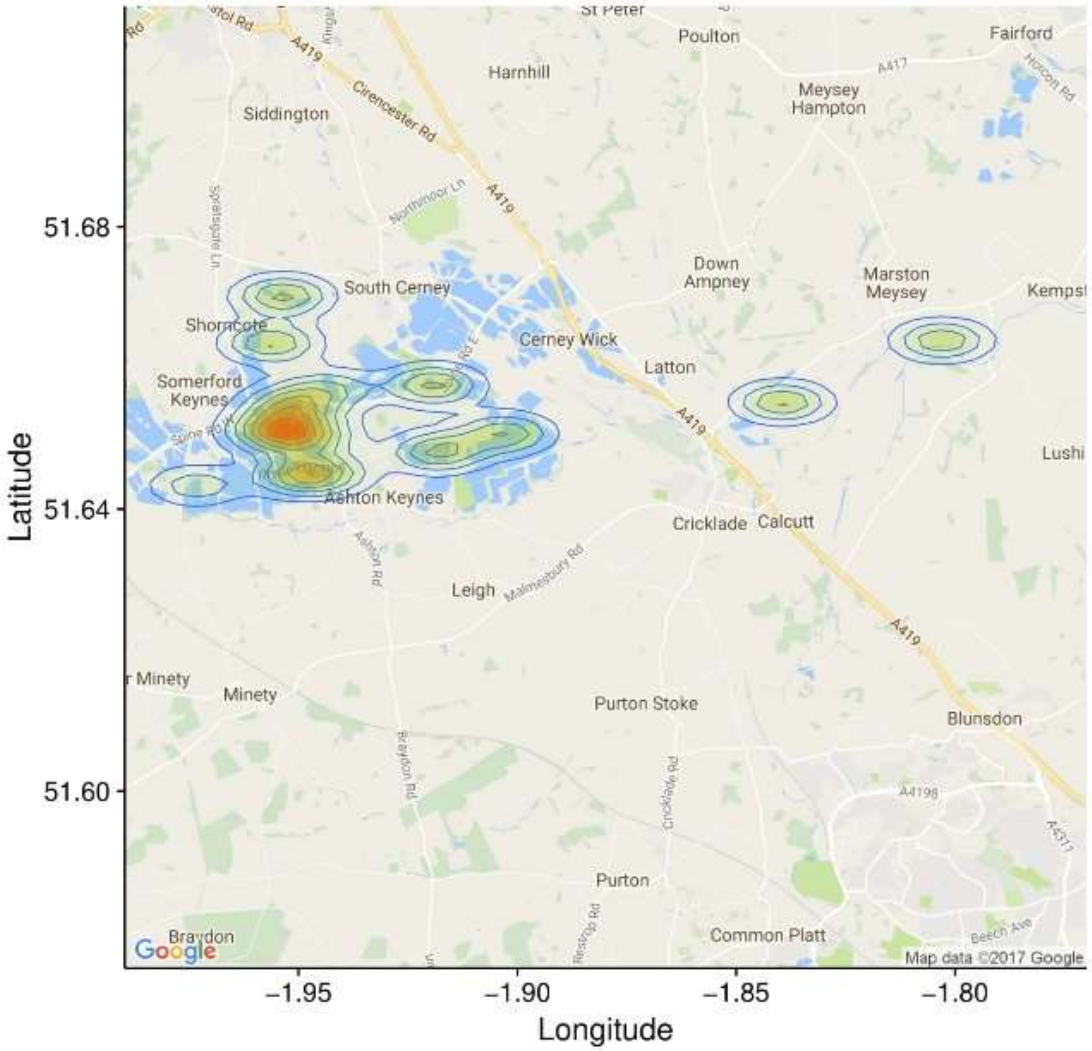
The area of disease spread could not be calculated for outbreaks in the spring movement network, since no simulation infected five sites, the minimum required to calculate home range area. The movement networks were largest in winter (35 sites), with 11 sites as nodes in the summer network and 21 in spring and autumn networks. However, the area covered by the sites was greatest in autumn (Figure 5.7). In spring, no single site was particularly prone to infection, whilst in summer and winter two-thirds of sites were infected in 70% of infections

(Figure 5.8). Three sites in both summer and winter movement networks were infected in 80% of infections, demonstrating their central position in the network.

a)



b)


Latitude
51.68
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−1.90
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−1.80
Longitude
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Poulton
Fairford
Meysey Hampton
Siddington
Cirencester Rd
A419
Northmoor Ln
South Cerney
Down Ampney
Marston Meysey
Shorncote
Cerney Wick
Latton
Somerford Keynes
Ashton Keynes
Cricklade
Calcutt
Leigh
Malmesbury Rd
Ashton Rd
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Purton Stoke
Blunsdon
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Purton
Braydon
Common Platt
Beech Ave
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Map data ©2017 Google

c)

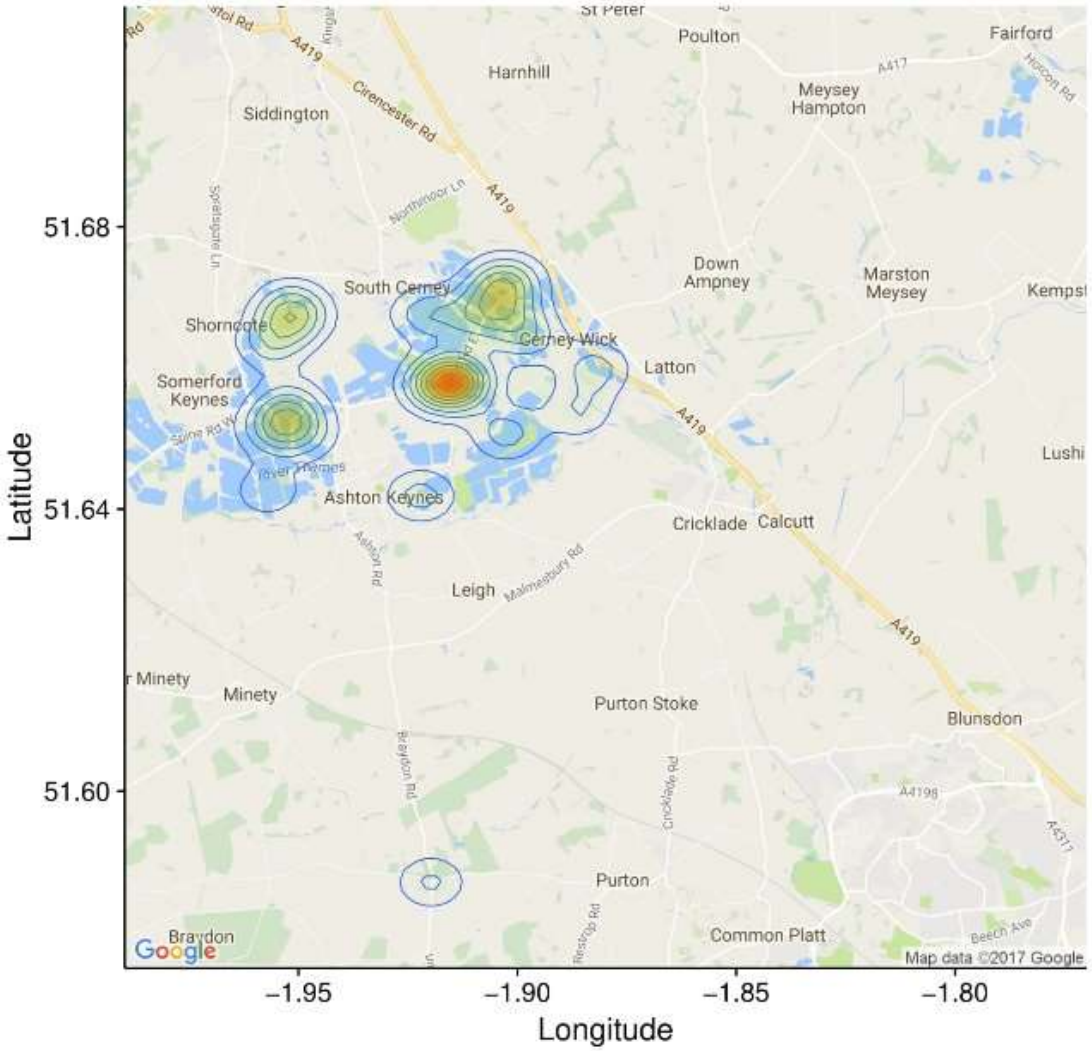


Figure 5.7. Area of simulated transmission in a) summer, b) autumn and c) winter in Cotswold movement networks. Heat map indicates sites repeatedly infected (red=highest frequency of infection, green=lowest frequency of infection).

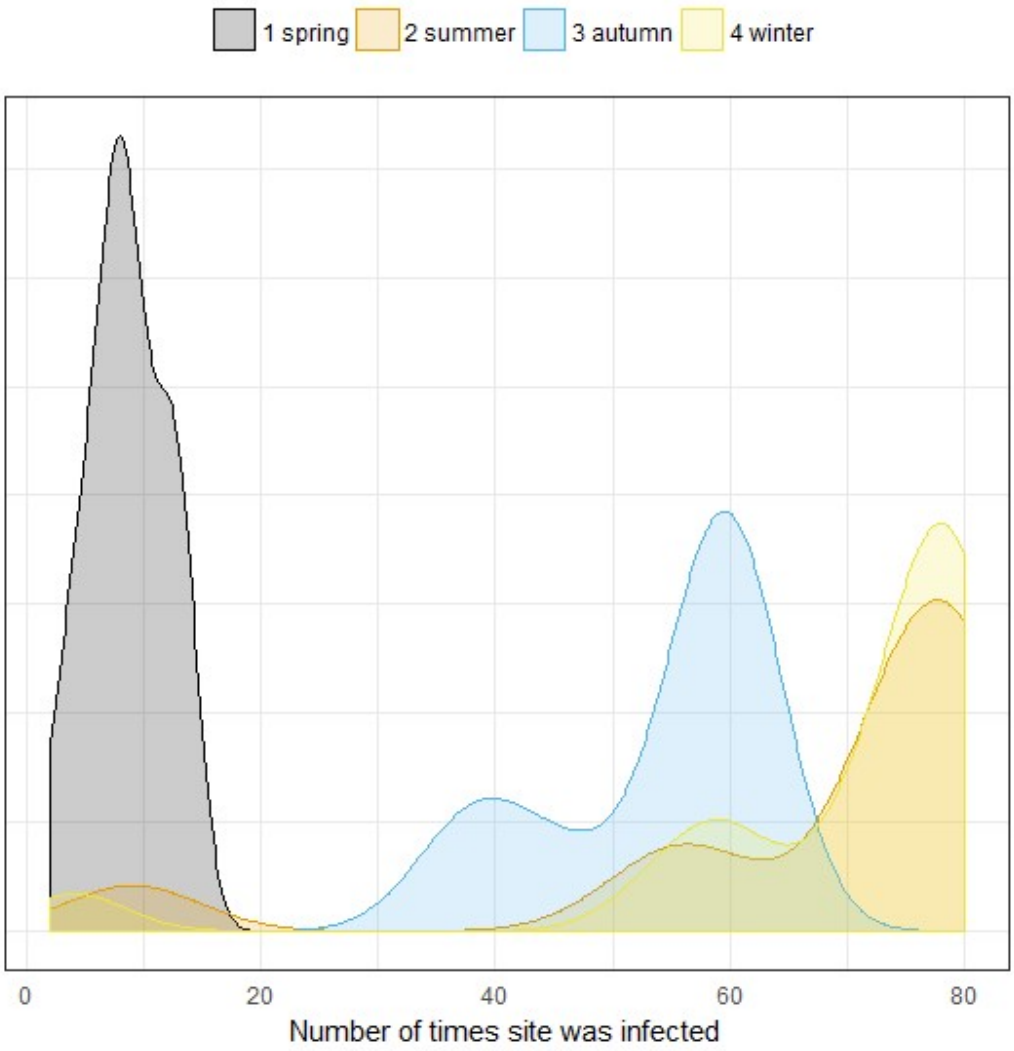


Figure 5.8. Number of times each site was infected in Cotswold movement networks. Broad distributions indicate seasons in which some sites were never infected and some were infected in most simulations. No site was infected more than 20 times in spring (and only few more than 10), whilst in summer, autumn and winter most sites were infected in multiple simulations, with 73% of sites infected in at least 70% of simulations in summer.

Higher transmission speeds were seen in the Cotswold seasonal networks than in the Thames networks in summer and winter, with similar mean infection speeds for both datasets in autumn, the post-moult period (Figure 5.9).

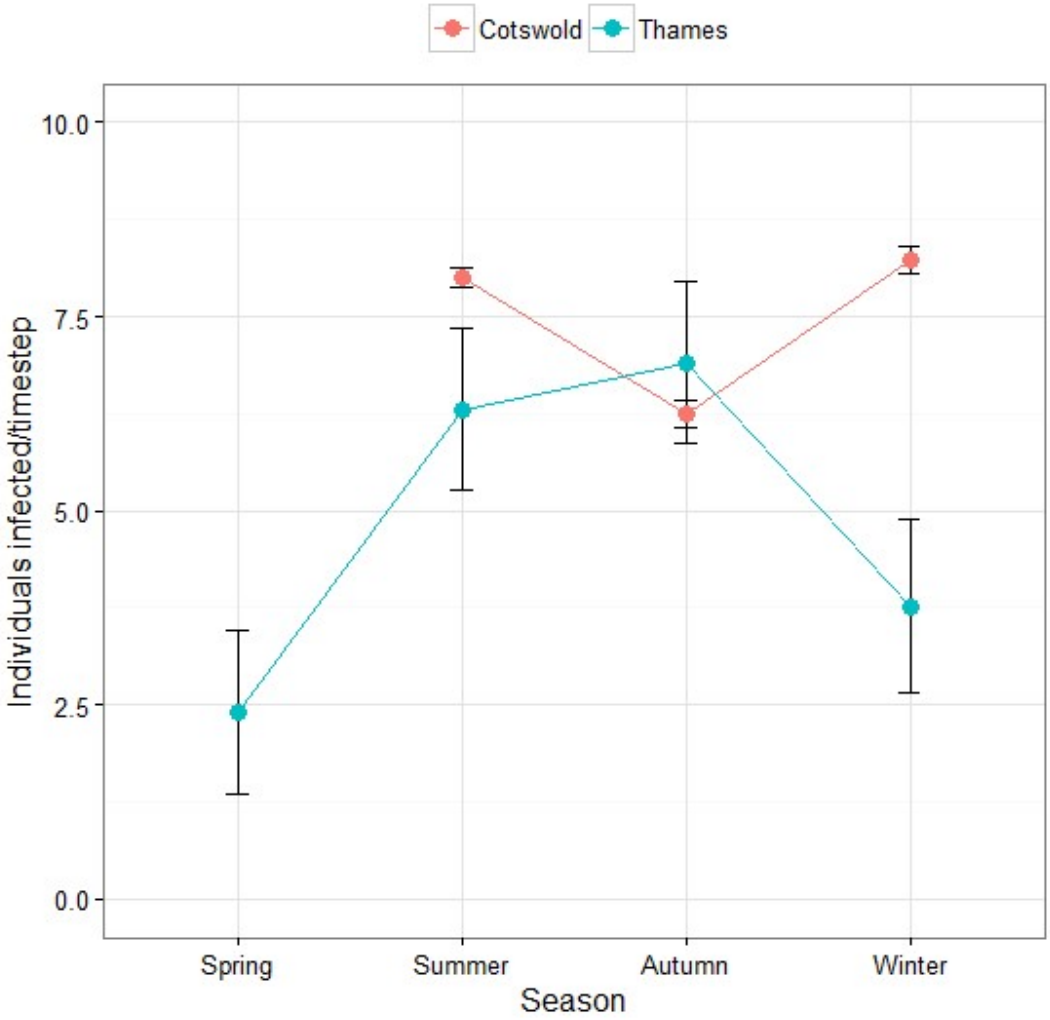
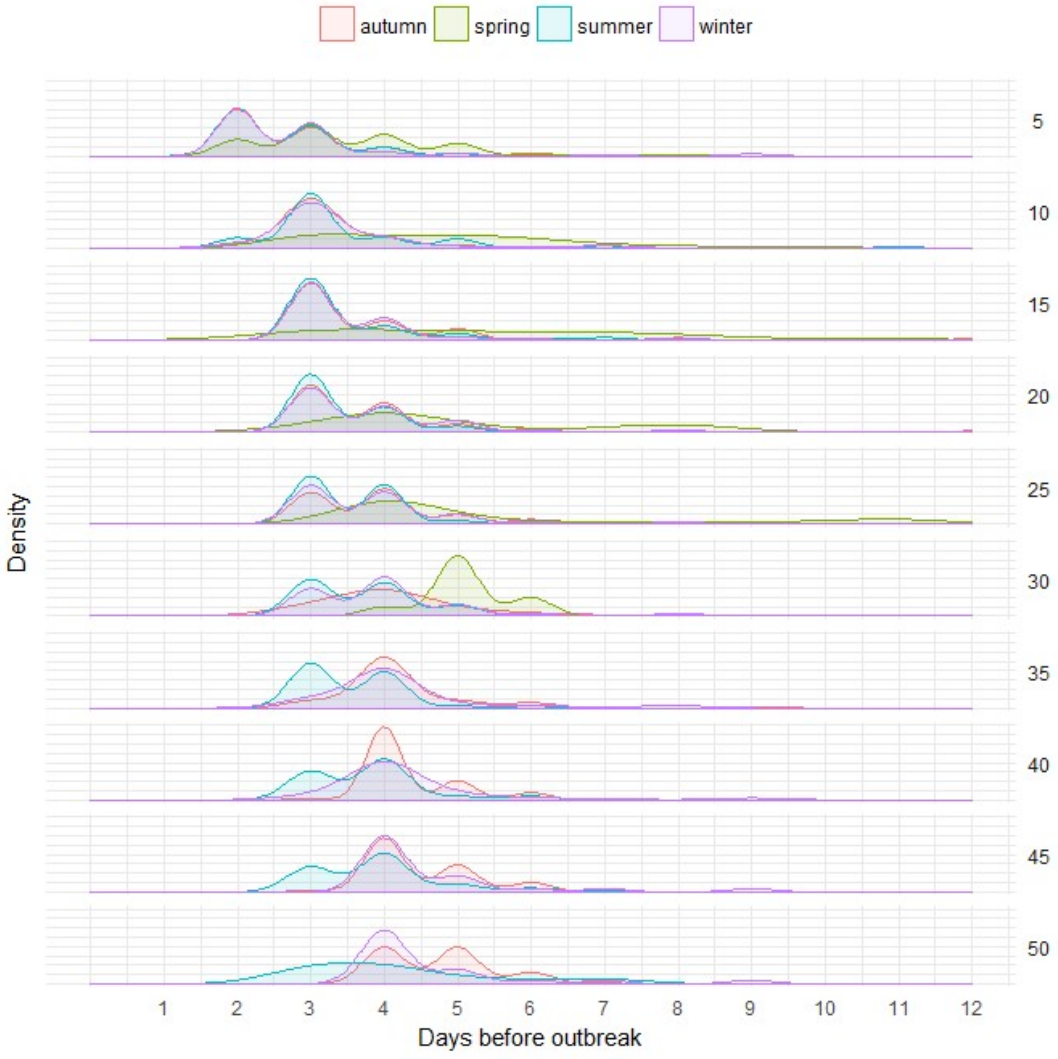


Figure 5.9. Mean transmission speed in Cotswold and Thames association networks.

Using these simulated data, the number of time steps before an infection triggered an outbreak was calculated to estimate the surveillance response necessary. Assuming the transmissible agent caused 20% mortality of infected individuals (100% mortality is possible for HPAI in poultry), and that passive surveillance would recognise an outbreak after the death of ten birds, the 50-bird outbreak threshold was breached within a week in summer, autumn and winter in both the Thames and Cotswold datasets (Figure 5.10).


autumn
spring
summer
winter
Density
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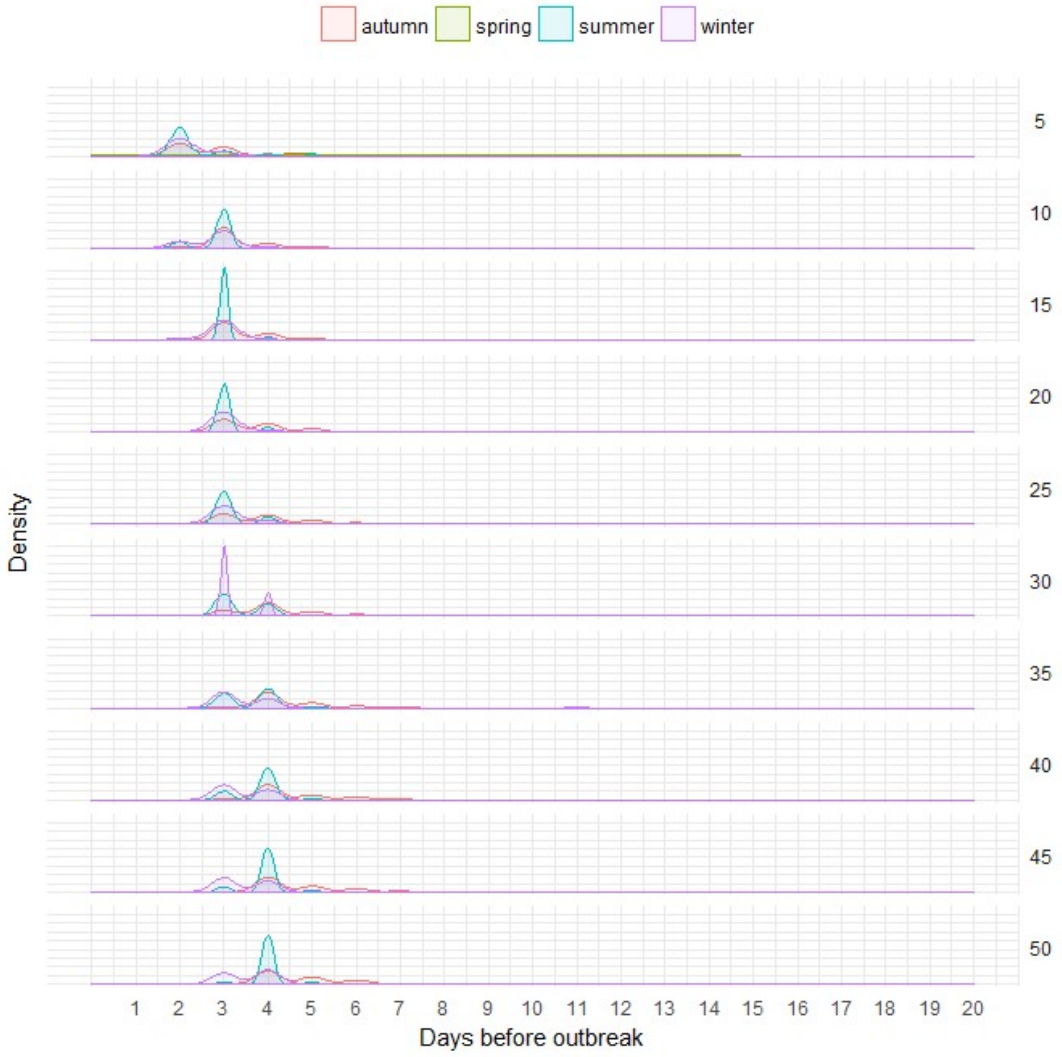
Days before outbreak

a)



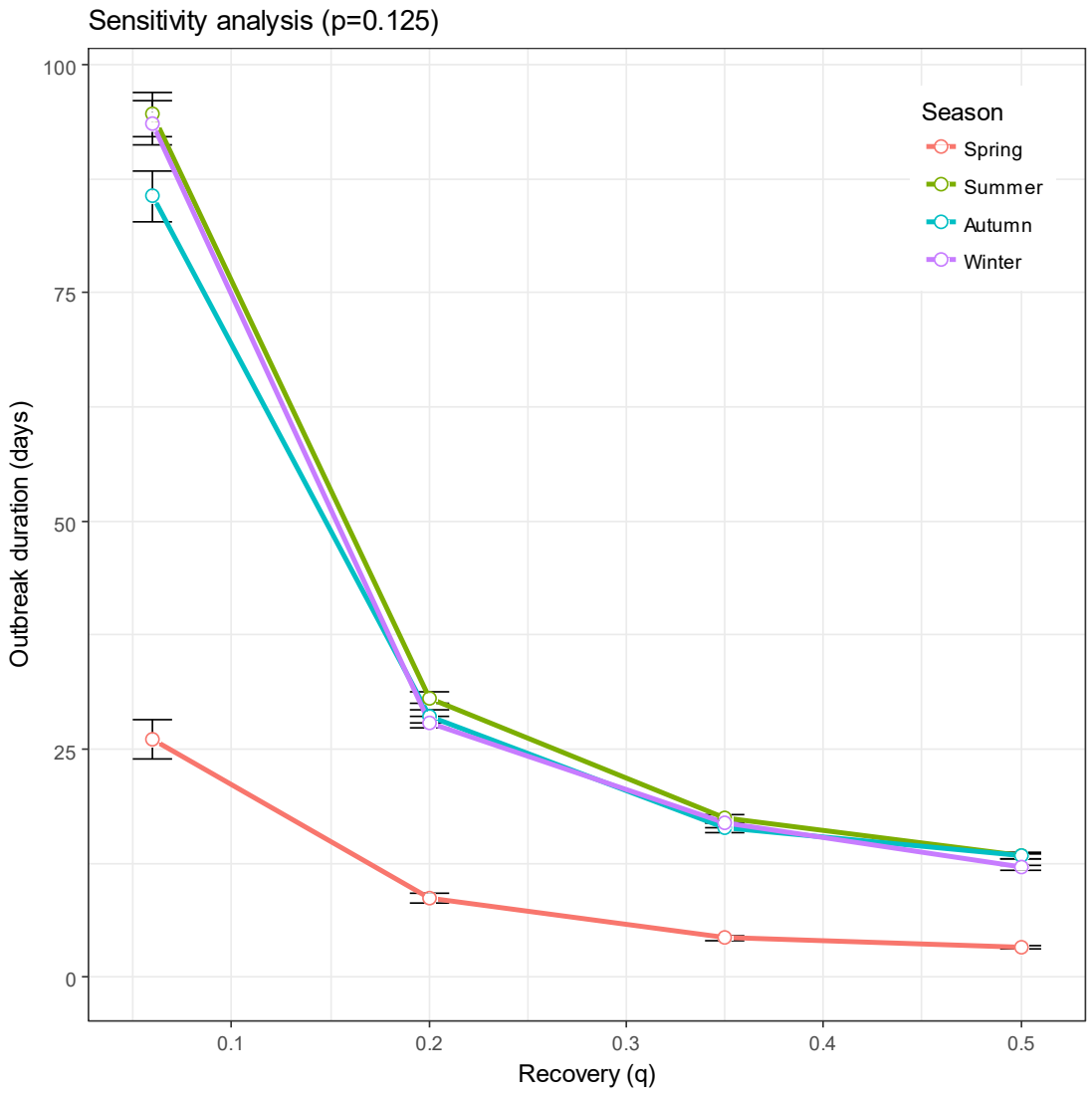
b)

Figure 5.10. Latency to outbreak in a) Thames and b) Cotswold association networks. Peaks shifting to the right as outbreak threshold increases indicates how, as the number of birds infected increases, it takes longer to reach the outbreak threshold. Again, density plots are interpreted as a smoothed histogram. NB: an outbreak threshold of ten infections was used in analyses.

Sensitivity analysis

For highly transmissible agents, simulated here as having infection parameter values of 0.25 and 0.5, changing the infectious period (defined by the recovery parameter, q) from 2 to 17 days affected outbreak duration only. Only at the lowest values of transmissibility (at values that are likely lower than seen naturally in this disease) did q influence the proportion of individuals infected (Figure 5.11).

a)



b)

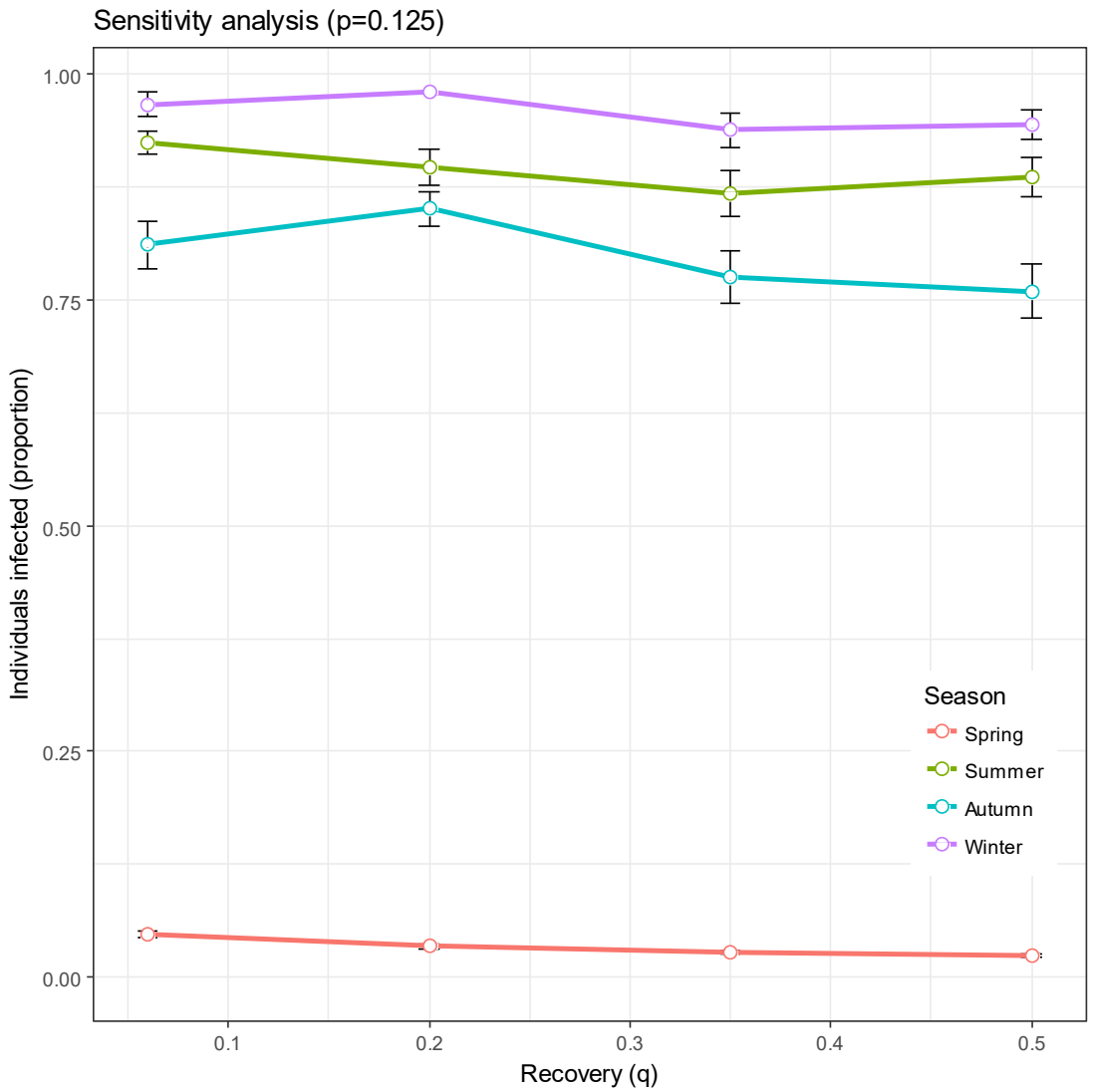


Figure 5.11. Impact of varying the recovery parameter (q) on a) outbreak duration and b) proportion of individuals infected in the Cotswold association networks.

5.5 Discussion

This study found the social networks of Canada geese to be extremely dense, as might be expected given the goose social system, and that the transmissible agent infected most of the network in fewer than five time steps in summer, autumn and winter. Despite the high modularity seen in all seasons (particularly spring, summer and winter), very few steps are needed to travel between any two connected nodes in the network in any season. In spring (Cotswold dataset) and summer (Thames dataset), networks were highly modular with several distinct clusters that were not connected, meaning that infection rarely triggered an outbreak (the infection of ten or more birds). In autumn and winter the high connectedness of the networks was demonstrated by the high proportion of infections that triggered outbreaks. Transmission was extremely rapid in all seasons and altering the transmission parameters did little to alter the proportion of the network infected. Increasing the recovery parameter did alter the duration of the outbreak by increasing the time it took for disease to leave the network.

The high connectedness of the association networks suggests that, in summer, autumn and winter, a large number of nodes would need to be removed to constrain disease transmission. In summer and autumn, removing 30-50% of nodes might prevent disease transmission but in winter it is not possible to give a minimum number of nodes required, such is the network's connectedness. The geographic networks of movements between sites demonstrate the seasonality of movement, with autumn and winter networks containing 100% and 200% more sites respectively than summer networks. In autumn and winter, high ranging meant that the area of disease spread was an order of magnitude greater than in other seasons. This study provides support for the hypothesis that transmission is swift through 'small-world' social networks (Guimarães et al. 2007). It suggests that a single infected bird could trigger an outbreak of 50 infected birds within days and indicates that the size of a disease outbreak is highly seasonal.

In the Cotswolds, combining association and movement networks allowed seasonality in contact rates and movement to be evaluated. In spring, contact and movement rates constrain transmission; in summer, contact rates facilitate but movement levels constrain transmission; and in autumn and winter both movement levels and contact rates facilitate transmission. The relationship between these two processes was not straightforward, with movement networks facilitating disease transmission over a large area in autumn and between a large number of sites (within a smaller total area) in winter. Firstly, this indicates that transmission peaks in the social network do not necessarily correlate with transmission peaks in the movement network. Secondly, this cautions that home range area is not always the most informative metric of movement behaviour and that small-scale movement is important in defining individuals' social networks.

In the Thames valley dataset, there was considerable variation in the seasonal pattern between years. Generally, transmission was lowest and slowest in spring and fastest and most complete in autumn. As in the Cotswold dataset, the time period between infection entering the network and it triggering an outbreak was relatively short: even where the outbreak threshold was set at 50 infections, infections triggered outbreaks within four days. The transmission peak in the Thames dataset association networks comes earlier than that in the Cotswold association networks: autumn rather than winter. This earlier peak in transmission could be a signal of network perturbation since this is a population that is subject to regular management, including culling during the summer moult in four of the five study years. If disruption of the social network caused increased mixing of birds and the re-establishing of social ties, it could trigger the rise in contact rates seen in the post-cull, post-moult period. In the Cotswold dataset, the autumn was a time of increased ranging movement but not increased transmission speed, suggesting that birds may be moving greater distances but doing so within their discrete social groups.

Transmission was lowest and slowest in spring in both populations. The low movement and highly clustered networks seen in spring could be protective in this species, constraining disease transmission just at the point a pulse of vulnerable new hosts enters the population. In the rest of the year, the high density of the Cotswold social networks means that the highly statistically significant differences in transmission rates between different seasons may not be biologically significant. When the vast majority of the network is 'infected' in under a week, the small differences between these seasons are more likely the result of a lack of error around simulated data rather than true biological differences. The lower transmission seen in the Thames population's association networks and the between year variation allows for greater distinctions to be made between transmission in different seasons. The proportion infected in summer and winter was variable, with autumn networks being most infected.

The mean number of individuals infected per time step was comparable across datasets and agrees with the reproduction ratio calculated from a poultry outbreak of HPAI H7N7 in the Netherlands in 2003 (Stegeman et al. 2004). Summer peaks in transmission in association networks have the potential to be detrimental to juvenile birds and those regaining condition following breeding and the moult.

The association and movement networks provide new hypotheses regarding transmission of agents with different modes of transmission. Diseases relying on close contacts between individuals are likely to be most transmissible in this system in summer. Meanwhile, diseases that primarily spread via fomites or the environment may be limited to a defined area in summer, since movement levels are low. By building up a picture of movement patterns at a landscape scale, and overlaying flock sizes and environmental conditions affecting persistence (e.g. salinity (Stallknecht et al. 1990; Brown et al. 2009)), one can predict more completely the risk of infection spreading from a site in a given season. Movement networks also reveal the sites that are prone to being infected during

disease outbreaks. In both summer and winter, the same sites were infected in over 70% of outbreaks. In spring, no site was infected in more than 20% of outbreaks. Thus, the movement networks suggest that sites that are infected repeatedly should be the focus of disease management efforts in summer and winter, whilst in spring and autumn, the impact of enforcing disease mitigation measures at any one site is less powerful.

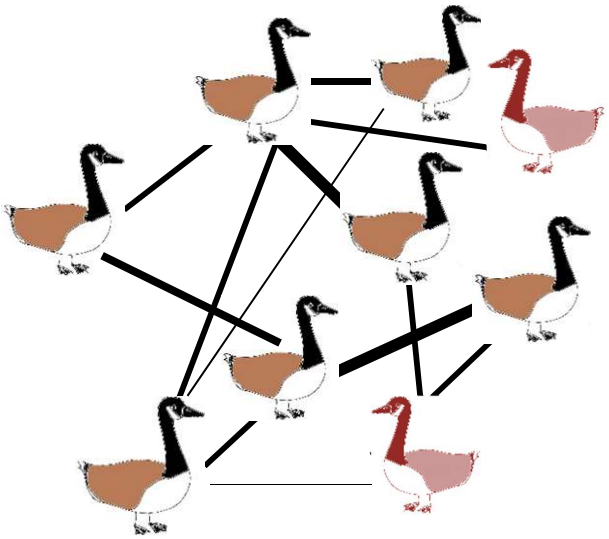
The high connectedness of these networks is demonstrated in the number of infections that trigger outbreaks and the insensitivity of the Cotswold dataset to the variation in the value of the infection parameter. This high connectedness presents a challenge for wildlife managers since it suggests that there are multiple links connecting clusters, with redundancy within each network. In this situation, where there are several possible routes of transmission, removing a single node or group of connected nodes is unlikely to prevent transmission. Even in seasons where movement levels are low, many network nodes would need to be removed to constrain disease transmission. The low latency to outbreak also suggests that passive surveillance would need to be rigorous, since there is little warning of outbreaks. In real time, transmission may be slightly slower since contacts will be clustered by time – in the networks used in the transmission simulations every connection exists all of the time. Time-ordered networks would provide a way in which to model this further, though these require a very high level of resightings (Blonder and Dornhaus 2011).

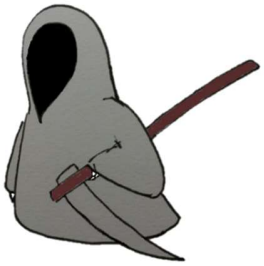
To return to the framework offered by Langwig et al. (Langwig et al. 2015), contact rates (association networks) and movement patterns (geographic networks) are only part of the picture. High environmental persistence of the high pathogenic avian influenza virus in cold conditions (Stallknecht et al. 1990; Brown et al. 2009) could amplify the peak in transmission seen in the winter and reduce the peak seen in summer association networks. Alternatively, the peak in transmission seen in the Cotswold summer association networks could be amplified by the presence in this season of naïve juvenile birds. The winter peaks

in disease prevalence observed in waterfowl (Newman et al. 2009) represent the in vivo situation once all mechanisms affecting transmission have been combined. Though this study does not explore seasonality in immune capabilities (Kortet et al. 2003; Mougeot et al. 2004; Hawley and Altizer 2011) or environmental persistence (Penczykowski et al. 2015), it provides support that in autumn and winter both contact rates and movement patterns facilitate the transmission of disease.

In conclusion, this study illustrates how association and movement networks might be used to infer disease transmission and the impact of seasonality on undisturbed (Cotswold) and managed, potentially disturbed (Thames) populations. It demonstrates that it would be necessary to remove a sizeable portion of the population in order to reduce transmission of any pathogen capable of spreading through direct transmission or the faecal-oral route (reflected by the association networks). Preventing access to certain sites or removing birds at those sites implicated by the movement networks may be possible to prevent transmission events and slow the speed of an outbreak. It is important, however, to understand the possible outcomes of management (such as culling or restricting access to a site) on bird movement and changes in association patterns.

6. Perturbing a social network: changes in social structure following a cull and their implications for disease transmission.





6.1 Abstract

The morality and ethics of culling are hotly debated. In order to evaluate the role of culls in wildlife management, wildlife managers require accurate information on the efficacy of culling in preventing disease outbreaks. Whilst culling reduces the numbers of available hosts, it may cause behavioural changes that promote disease transmission. The outbreak-enhancing effects of culling need to be offset by the outbreak-reducing effects for culling to be an appropriate response to disease outbreaks, yet the size and impact of culling on social behaviour is not fully understood. This study found survivors of a partial cull to range less far and contact fewer birds in the year following the cull than birds that were not present at cull sites. Losing close associates correlated with birds increasing their association strength to surviving associates. However, networks were more fluid and homogeneous in the three months immediately following the cull, suggesting that social structures were disrupted during this time. These findings suggest that, in Canada geese, culling during the post-breeding moult may be an appropriate method by which to reduce the size of outbreaks with a winter peak. However, it may increase the spread of disease outbreaks in the immediate post-moult period.

6.2 Introduction

Social network analysis, which quantifies the nature and strength of relationships between individuals, is increasingly being used to understand how an individual's patterns of association contribute to population-level processes (Downing and Royle 2013). The structure of the social network has been found to influence long-term fitness (Royle et al. 2012), the transmission of information on the location of food sources (Aplin et al. 2012) and the spread of learned behaviours (Mann et al. 2012), all of which are of interest when managing populations. Importantly, social network analysis has also advanced our understanding of the transmission of disease in wild systems (Hamede et al. 2009; Craft et al. 2011; Vanderwaal et al. 2013; Reynolds et al. 2015) and has been used by wildlife managers to understand the ways in which vaccination and targeted removal programmes may affect populations (Rushmore et al. 2013; Rushmore et al. 2014; Wilson et al. 2015). However, one crucial aspect that remains unclear is the effect of management interventions on social network structure itself. Little is known about how management interventions such as culling, which may affect ranging behaviour (Tuyttens et al. 2000) and disrupt social hierarchy (Bierbach et al. 2014), may alter social behaviour and thus social network structure. Social network analysis can provide the key to understanding the implications of anthropogenic or natural social network disruption. An understanding of social behaviour may be important for the development of disease control strategies, in particular allowing wildlife managers to judge whether interventions such as culling are likely to reduce disease transmission.

Disruption of the social network as a result of the removal of individuals or substantial changes in individual social behaviour is termed perturbation. Such perturbation may be the result of natural events that remove individuals and remix groups, but is often cited as the result of human interventions, such as those to reduce population numbers (culls) or supplement them (reintroductions) (Mittelbach et al. 1995). In the face of disease outbreaks in wildlife that have the

potential to cause disease in humans or domestic animals, culling is one of several potential management options (Allan and Feare 1994; Hallam and McCracken 2011). Though experimental evidence from natural systems is rare, removal of individuals has been found to cause increased movement levels and contact rates amongst surviving individuals (Tuyttens et al. 2000; Woodroffe et al. 2006; McDonald et al. 2008), the dissolution of social groups (Borg et al. 2015) and disordered social hierarchies (Bierbach et al. 2014). In the European badger (*Meles meles*), culls were found to alter the ranging behaviour of individuals and resulted in the disruption of previously stable ranges (reviewed by (Carter et al. 2007) , increased overlap in ranges and sharing of latrine sites by badgers from different social groups. Crucially, these altered movement patterns correlated with increased levels of bovine TB infection in cattle in the area surrounding the cull, thought to have arisen as a result of enhanced badger movements (Woodroffe et al. 2006). Even non-lethal management of movement behaviour may alter contact rates: In sleepy lizards (*Tiliqua rugosa*), introduction of impermeable barriers to alter the geography and force changes in movement patterns introduced more routes for disease transmission through the network (Leu et al. 2016). Such studies suggest that culls that are intended to control disease levels, could, in some circumstances, be ineffective (Beeton and McCallum 2011; Hallam and McCracken 2011) or even exacerbate disease transmission by substantially altering the social network.

Even without increasing movement levels, cull-induced social network perturbation may potentially facilitate the spread of infection. Many animal and human systems show network structures that resemble ‘small-world’ networks (Watts and Strogatz 1998). Individuals in small-world networks are strongly connected within their social group (or ‘cluster’) by their frequent associations or interactions, and linked less strongly to other clusters. Small-world networks have been observed in ungulates (Grevy’s zebra, *Equus grevyi,* and Indian wild ass, *Equus hemionus khur*, (Sundaresan et al. 2007)), lions (*Panthera leo,* (Craft et al. 2011)), takahe (*Porphyrio hochstetteri*, (Grange et al. 2014)), guppies (*Poecilia*

reticulata, (Croft et al. 2004)) and Canada geese (*Branta canadensis*, chapter 1). There is theoretical evidence suggesting that infection spreads quickly through these networks (Moore and Newman 2000; Saramäki and Kaski 2005), but that high levels of clustering of individuals into discrete communities can be protective (Christley et al. 2005). This protection stems from the network structure since even when disease saturates one cluster it may not be transmitted further, thus sparing other clusters. This protective characteristic of clustering may be particularly relevant for pathogens requiring intimate contact or prolonged exposure, such as sexually transmitted infections (De et al. 2004) or tuberculosis (Porphyre et al. 2011). It seems likely that perturbations such as culling could lead to networks losing highly clustered structures and becoming more homogeneous (Bierbach et al. 2014). Transmission may be slower and more predictable through a homogeneous network but all of the individuals within it become at risk of infection from multiple directions.

Since any intervention will only affect a subset of the population, it is important to establish whether the effects of any subsequent perturbation extend beyond this group. Dominance in many social systems is linked to the number of close associates (Poisbleau et al. 2006; Poisbleau et al. 2008) and any reduction in numbers is likely to alter dominance ranking, which may disrupt social structure. In addition, in many grazing species, there may be advantages to maintaining ties with the same associates through social vigilance (Favreau et al. 2010) or competitive interference (Bijleveld et al. 2012). Furthermore, the sensitivity of social species to partial culling is not known. Large and small social groups would be equally at risk of dissolution if losing a certain percentage of the social group causes dissolution of the cluster. However, only small social groups would be affected if culling exerts a threshold effect, whereby below a certain number of individuals the group ceases to function. In wolves (*Canis lupus*), removal of individuals caused dissolution of groups, but only when the individuals removed were part of the breeding pair and only when pack size was low (Borg et al. 2015). If perturbation does cause the dissolution of clusters, culling for disease

control could result in infected individuals contacting new naive individuals, spreading disease more widely. Therefore, in order to manage wild populations effectively it is important to know whether culls intended to reduce disease levels may disrupt social structure in ways that are counter-productive for disease control.

Canada geese present an ideal study system in which to understand the effects of perturbation on social species. Most species of geese of the genera *Branta* and *Anser* are highly social and gregarious at times during their annual life cycle. They have a structured social system arising from the number of close associates, with families dominant over pairs, and pairs over unpaired birds (Poisbleau et al. 2006). These groups of close associates aggregate in flocks of up to several hundred individuals. As a species that shares sites with both migratory and domestic bird species, and with human activities, they are of interest because they carry a diverse selection of important pathogens (Feare et al. 1999; Bonner et al. 2004), including Newcastle disease (Bonner et al. 2004) and *Helicobacter* species (Fox et al. 2006), with opportunities for onward spread.

Being both an invasive species in the UK and a potential public health risk (Allan and Feare 1994; Dieter et al. 2001), Canada geese are frequently managed by culling, which typically consists of either shooting of individual birds in winter or culling of flightless flocks in the summer moult. Different types of cull may disrupt the social network to different degrees. Shooting removes small numbers of individuals that are unlikely to be from the same social group; an intervention that, if it causes disruption, would affect individuals across several social groups. Moult catches, in which large groups of flightless birds are rounded up, remove complete social groups and thus have a profound impact on some groups whilst leaving others potentially unperturbed.

The present study will determine global network structure and movement behaviour in a population of Canada geese managed by culling, making it the

first comparison of social network structure pre- and post-perturbation in a free-living population. Perturbation is predicted to affect individuals' ranging behaviour, making them range further and, in the case of birds that had close associates removed, cause the formation of new affiliations. This increased mixing will be evident in alterations to home ranges, increased movement propensity and the formation of new connections (or strengthening of weak connections) in the network following perturbation. Divorce rates have been noted to increase in many pair-bonded species following brood failure (Dubois and Cézilly 2002) so partial removal of the group's members may trigger a corresponding behaviour in the remaining birds causing them to disperse and join other social groups, as seen in wolves (Borg et al. 2015).

Culling is predicted to lead to higher movement levels (which may bring changes in site use) and the fracturing of established ties. At the population level, enhanced movement and contact rates would be expected to increase the number and frequency of connections between groups in the network. This would lead to the post-perturbation network comprising more groups (communities or clusters in network parlance), shorter path lengths and individuals with both higher and less variable numbers of associates. However, if each individual has a sufficiently high number of preferred associates, the network may be robust to the removal of individuals since groups will reform without the missing birds. Where social networks are robust, culling may not lead to any changes in behaviour.

In the present study we compare network-level metrics that together quantify how heterogeneous and highly structured the network is before and after the intervention, and explore whether social groups visible in the network prior to intervention are visible afterwards, as would be predicted if birds maintained their associates rather than abandoning them. We then ask whether individuals are repeatable in their affiliations, range further, overlap their ranges more, use more sites or make more new associations following the intervention if they were

present at a cull site. We examine the effects of social proximity to culled birds and geographic proximity to cull sites on these behaviours. Finally, we ask whether losing a proportion or a threshold number of individuals from the social group better predicts how many pre-cull associates individuals retained (Borg et al. 2015).

6.3 Methods

Study system

The study area within the Cotswold Water Park (CWP), UK, (Ordnance Survey grid reference SU 0796) consists of working and restored gravel pits covering 85 km^2 near Cricklade, Wiltshire (OS grid reference SU 0985 9357). The 140 waterbodies are largely privately owned and managed, primarily for water sports and angling, but the CWP Trust oversees the area (which includes land in Wiltshire, Gloucestershire and Oxfordshire) and has the role of recording and advising on biodiversity and wildfowl management within the park. The lakes are surrounded by farmland, nature reserves, holiday accommodation and small settlements. Canada geese are resident at this site all year round with a wintering population in excess of 600 (Holt et al. 2015). The combination of numerous water bodies bordered by amenity grassland and arable fields provides much suitable habitat for this invasive species. The population has been controlled in recent years by regular egg oiling (February-April) and sporadic shooting (September-January).

UK-resident Canada geese form flocks consisting of 3-400+ birds depending on season and region. During the breeding season (March-June), breeding pairs split off and defend territories, whilst non-breeding birds remain in flocks. Canada geese moult their flight feathers, annually timed to follow breeding. During the moult, breeding pairs, offspring and non-breeders congregate together in moulting flocks. This flightless period extends from June into July, when entire flocks can be caught.

In order to mark individual geese, five moult sites distributed across the CWP, (with a maximum geodesic distance between sites of 16.93km, and a minimum of 1.61km) were identified as catch sites (Figure 6.1). On 3rd and 4th July 2012

geese were rounded up on the water by an experienced team of kayakers and driven on shore and into a screened pen. Individual birds were then taken from the pen and fitted with highly visible neck collars bearing unique codes and metal British Trust for Ornithology (BTO) leg rings in accordance with local ringing practices. Neck collars (dimensions: inner diameter = 42mm, height = 65mm) were produced by Interrex and were formed of black plastic overlaid with orange, so that the two-letter codes appeared as black text on an orange background. In total, 153 adult birds were fitted with collars. In 2013 the process was repeated at six sites (Figure 6.2) and an additional 39 collars were fitted.

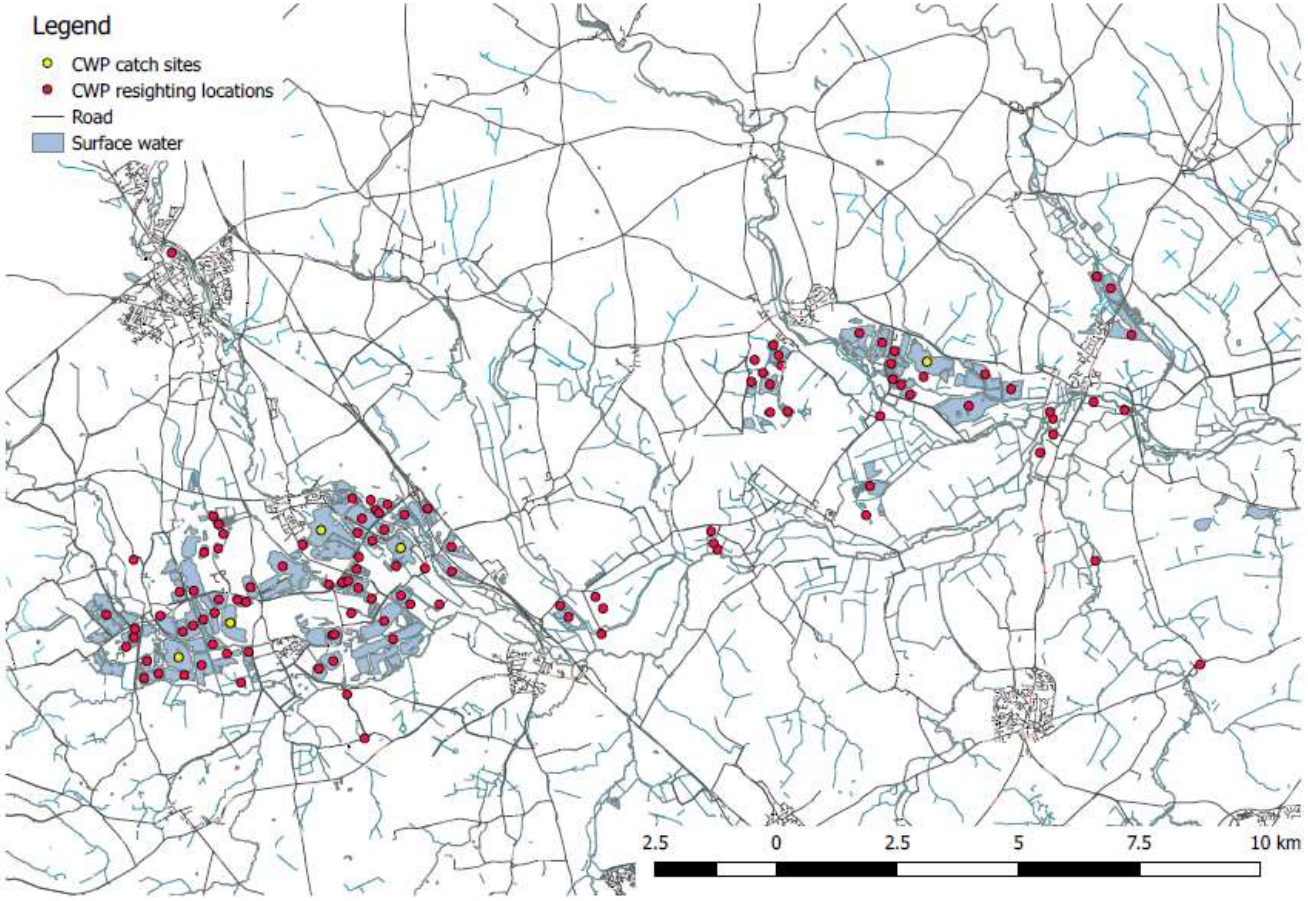


Figure 6.1. 2012 catch sites at the CWP.

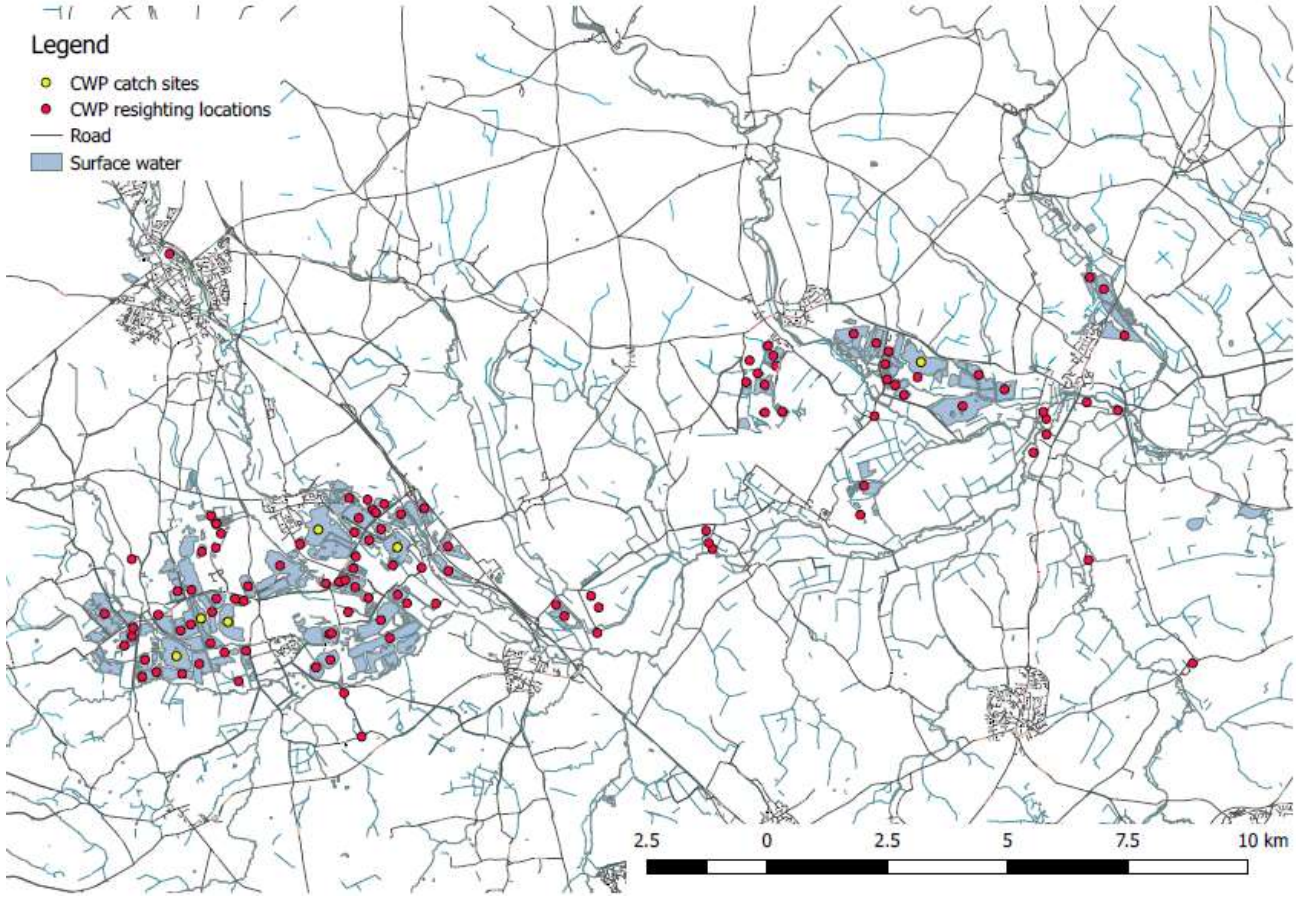


Figure 6.2. 2013 catch sites at the CWP.

Experimental perturbation of the population

Moult flock roundups took place at six sites over two days in 2013. These took place under licence with Natural England as part of a wider goose management plan. At the three non-cull sites, all birds were released. During the removal operation, 39 adult birds were removed from the three cull sites, representing 50-66% of the birds present at those sites and 20% of the birds present at all sites (n=189). Collared and ringed (n=16), ringed (n=2) and unmarked (n=21) birds were removed.

At non-cull sites, marked birds' rings and identifying marks were recorded where present and replaced if necessary. All unmarked birds were marked with metal BTO leg rings and unmarked adults were fitted with plastic neck collars. After processing, birds were released back onto the water body from which they had been taken. Goslings were processed first and released in a group with several accompanying adults.

At cull sites, adult birds were removed from the holding pen by a handler and directed alternately into one of two processing streams by the scribe (who did not view the bird). Only adult birds were present at cull sites: sites containing goslings were designated non-cull. Birds in the first processing stream underwent the same processing as birds from non-cull sites and were released. Birds in the second processing stream were taken to a screened area and dispatched by lethal injection of pentobarbitone into the wing vein, administered by a trained and competent animal technician.

Construction of the networks

Collar codes of marked individuals were recorded in the field by an observer with binoculars and a telescope. Group membership, location, flock size, time and date were also recorded. Resighting of the marked birds took place in every month from July 2012 to June 2014, from dawn to dusk on 291 days.

Birds in a flock present at the same site at the same time were judged to be associating according to gambit of the group (Franks et al. 2010) and each of these group associations was termed an ‘event’. The extent of flock membership was determined by a chain rule based upon local geography and the distances between birds – birds were considered to be within a flock if they were in visual contact, were not separated by barriers such as hedges or by distances four times greater than the mean inter-individual distance (measured in goose body-lengths to allow accurate calculation of distances at distance). On water bodies, all individuals present on the lake were termed associating. In fields or other areas away from water, groups of geese tended to stay away from field margins or boundaries and self-organised into cohesive flocks. All fission-fusion events were recorded, and small groups of individuals that arrived or departed separately from the main flock were recorded both as part of the large flock and as a subunit in a separate ‘event’.

A matrix of these co-occurrences was then used to calculate an index measuring strength of association between birds. The half-weight index is commonly used in social network analysis for the construction of social networks where nodes are more likely to be observed when not associated, or when not all individuals can be identified (Whitehead 2008). The half-weight index assigns each pair of individuals an association strength based upon the number of times they are seen together (x) versus separately in different periods (y_A+y_B) or separately in the same period (y_{AB}).

$$\text{Half-weight index} = x/(x+y_{AB}+1/2*(y_A+y_B))$$

Both whole-year and seasonal association networks were calculated (Table 6.1). Whole-year networks ignore seasonal variation and look for overall patterns of association and network position across the year. Seasonal networks reflect differences in social behaviour within the year.

Table 6.1. Resightings used in construction of seasonal networks and calculation of metrics.

Network	Time period	Days	Events	Resightings (individuals)
Whole year pre-cull	June 2012 – July 2013	138	399	3212 (153)
Whole year post-cull	July 2013 – July 2014	153	415	2473 (159)
Moult 2012	June – July 2012	13	69	880 (153)
Post-moult 2012	Aug – Oct 2012	23	55	320 (126)
Winter 2012-2013	Nov 2012 – Feb 2013	52	175	1523 (142)
Breeding 2013	Mar – May 2013	55	36	87 (58)
Moult 2013 (pre-cull)	June – 2nd July 2013	16	47	402 (100)
Moult 2013 (post-cull)	3rd July 2013	9	51	684 (119)
Post-moult 2013	Aug – Oct 2013	41	127	1047 (150)
Winter 2013-2014	Nov 2013 – Feb 2014	46	102	355 (129)
Breeding 2014	Mar – May 2014	44	110	258 (84)
Moult 2014	June – July 2014	14	26	129 (74)

Calculation of social network metrics and a bipartite network

Path length, modularity and mean degree were calculated in R (version 3.2.0, package ‘sna’) for seasonal and whole-year networks.

Path length is a measure of how many steps exist between each pair of nodes within the network (West 1996). Longer path lengths indicate that there are fewer shortcuts through the network and that transmissible agents may take longer to saturate the network. Here, mean path length (mean of all paths between each pair of nodes within an unweighted network) was calculated in R (version 3.2.2, package ‘igraph’).

Modularity was calculated for each network using the walktrap algorithm (R, version 3.2.2, package 'igraph' (Csardi and Tamas 2006)), which is a community detection algorithm used to assign individuals to social clusters based on their position in the social network (Clauset et al. 2004). Modularity algorithms divide networks into clusters by separating nodes from those with whom they have fewer connections than would be predicted, and grouping them with nodes with whom they have more connections than predicted. The algorithm continues until it would be separating nodes with equal connections to nodes within and without their cluster. At this point each cluster is an indivisible subgraph (Newman 2006).

Degree is the number of other nodes to which the focal node is connected: here the number of individuals with which the focal individual associated. Both a vector of individuals' degree and a mean degree value were calculated for each network.

To establish the extent to which clusters fractured as a result of individuals changing social group following the cull, a bipartite, weighted, directed network (Albert et al. 2002) was constructed. In this, nodes represent the social groups in years one and two (calculated using the walktrap clustering algorithm, (Csardi and Tamas 2006)). Edges between nodes represent movement of birds between social clusters, weighted by the number of birds that moved from each group in year one to each group in year two. Social groups in year one were named with numbers (1-5) and social groups in year two were named with letters (A-N). However, the order of groups' names carried no significance i.e. group one in year one did not necessarily relate to group A in year two. Birds that were removed in the cull and those not seen in year two were placed in separate clusters ('removed' and 'unknown').

Calculation of movement behaviour

Movement behaviour for each whole year of resightings was measured in three ways: number of sites used in each year, calculation of home range area in each year and home range overlap between years.

Firstly, the number of sites used by each bird over the year was calculated. This small-scale measure distinguishes between birds that frequently moved between geographically close but separate lakes. Sites were defined as single lakes or fields, within which there were no barriers (vegetation, fences) that would prevent birds from being out of visual contact with others at the site, or that would prevent free movement by the birds walking across the site. This value was normalised by taking the residuals from a linear regression of number of sites/number of observations and adding them to the mean, resulting in a corrected value giving the number of sites used for the known number of observations.

Secondly, each bird's core 20%, 50% and 95% home ranges were calculated to give a better understanding of the area used by each bird over the year, in line with previous research (Baracchi and Cini 2014). Home ranges were calculated by assigning latitudes and longitudes to all observations of each bird. These points were then used to calculate utilisation distribution (UD) kernel estimations (Worton 1989) in R (version 3.2.2, package adehabitat (Calenge 2006)), which calculates not only the total home range but also the percentage of the range used most heavily; the area in which, from the mapping of all observed locations, the individual occurred most frequently. The home range area in each year (at the 95% UD level (Riordan et al. 2011)) was then used to calculate the change in range shown by each bird in the post-cull year. Since range was subject to high levels of individual variation, the proportion of range change and the direction of change (positive or negative) was used rather than raw values.

Finally, overlap in home ranges was calculated using the home range (HR) method in R (version 3.2.2, package adehabitat (Calenge 2006)). In this, the

area of overlap in ranges is calculated as a proportion of the second year's home range, i.e. HR[i,j] = A[i,j] / A[i] (where A[i,j] is the overlap area between years and A[i] is the second year's home range area (Fieberg and Kochanny 2005)). This analysis involved birds with at least five resightings in each year. The home range method was chosen for calculating overlap because it coped better than other suitable methods (e.g. the utilisation distribution overlap index (Fieberg and Kochanny 2005)) when calculating overlap between ranges differing by several orders of magnitude. One bird present in both years (code JC) was excluded from analyses because all resightings were recorded within too small an area for overlap to be calculated.

Statistical analysis

The fragmentation of the social network following the cull was described by calculating each network's modularity and comparing observed modularity scores to those of theoretical networks. The observed post-cull network modularity scores were compared with those of i) random networks assuming no preferential associations, ii) networks assuming associations only between previous associates and iii) networks with links only between frequent associates (those within the same pre-cull social cluster). The error around modularity estimates was assessed using resampling with replacement (bootstrapping) (Whitehead 2007). The observed modularity values were then compared with those arising from theoretical networks created from three different datasets: a dataset resampling from an unconstrained edgelist (containing every potential pair of individuals, or dyad, and the weight of their association) of every potential edge within the population; a dataset resampling from an edgelist constrained so that only realised edges (those with positive weights) were included; and a dataset resampling from an edgelist containing only those edges belonging to birds of the same pre-cull social cluster. In each case, the dataset was resampled 1000 times and modularity recalculated for the resultant network.

A bootstrapped t-test performed in R (version 3.2.2), cross-checked with a social-network-specific t-test run in UCINET (Borgatti et al. 1999), was used to compare mean degree between years. Mean degree was calculated for birds present in both years only.

Social cluster persistence was analysed at an individual level using model selection by AIC of candidate variables from a range of candidate linear mixed models constructed in R (version 3.2.2, packages MuMIn (Barton K 2009), lme4 (Bates et al. 2015) and lmerTest (SAS Institute 1978)). This approach was designed to determine differences in group composition before and after the cull. It assessed individuals' retention of associates by asking how the number and proportion of known associates in their post-cull social group correlates with presence at a cull site and the overall composition of the post-cull social group (Table 6.2). We hypothesised that perturbation of the social network would result in birds from cull sites retaining fewer associates. Model selection using AIC is robust towards the inclusion of less-useful terms when trying to distinguish between several competing hypotheses (Richards et al. 2010). Models within four AIC units of the best-fitting model were taken to be equivalent.

Table 6.2. Terms used in candidate set of linear mixed models of cluster dissolution.

Dependent variable	Explanatory variables	Type		
Proportion of associates from pre-cull social cluster retained in post-cull cluster	Number of birds in post-cull cluster	Predictor	Fixed	Discrete
	Proportion of new associates in post-cull cluster	Predictor	Fixed	Continuous
	Proportion of associates removed in the cull	Predictor	Fixed	Continuous
	Present at a cull site	Predictor	Fixed	Categorical
	Present at a cull site* Proportion of new associates in post-cull cluster	Predictor	Fixed	Interaction
	Present at a cull site* Proportion of associates removed in the cull	Predictor	Fixed	Interaction
	Social cluster in year 1	-	Random	Categorical
	Social cluster in year 2	-	Random	Categorical

Ranging behaviour following the cull was analysed in three statistical stages. Firstly, an exact binomial test in R was used to establish whether birds increased their range in 2013-14 relative to 2012-13. Secondly, a generalised linear model with a binomial distribution to determine whether birds proximate to the cull (those closely associating with a removed bird or geographically close to a cull) were more likely to increase their ranges than those further away. In this, the proportion of range change for each bird was modelled using a linear mixed model with a binomial error distribution to examine differences between the direction of range changes for cull-site and non-cull-site birds (Table 6.3). Thirdly, birds that increased their range were included in three linear mixed models to examine how social and spatial proximity to the

cull affected the extent to which movement changed. Movement propensity (number of sites used), range area increase and range overlap between years were all analysed using linear mixed models in R (version 3.2.2, packages 'lme4' (Bates et al. 2015), 'lmerTest' (SAS Institute 1978)), Table 6.4.

Table 6.3. Terms used in linear mixed binomial model to identify correlates of changes in range size.

Dependent variable	Explanatory variables	Type		
Increase in home range	Moulted at a site contiguous with a cull site (spatial/treatment)	Predictor	Fixed	Categorical
	Moulted at a cull site (spatial/treatment)	Predictor	Fixed	Categorical
	Connection strength to removed bird (social)	Predictor	Fixed	Continuous
	Moulted at a site contiguous with a cull site * Connection strength to removed bird	Predictor	Fixed	Interaction
	Moulted at a cull site * Connection strength to removed bird	Predictor	Fixed	Interaction
	Moult site 2013	-	Random	Categorical

Table 6.4. Predictor terms used in linear mixed models to identify correlates of changes in movement propensity, range size and overlap.

Dependent variable	Explanatory variables	Type		
Movement propensity: change between years in number of sites used (corrected in each year for number of observations)	Social distance: maximum connection strength to a removed bird	Predictor	Fixed	Continuous
	Geographic distance: sum geodesic distance from bird's moult site to all three cull sites	Predictor	Fixed	Continuous
	Presence at cull site: two-level factor indicating presence or absence at a cull site	Predictor	Fixed	Categorical
	Moult site in cull year	-	Random	Categorical
Home range increase: % increase in home range (95% UD) / Home range overlap: overlap of pre-cull with post-cull range (both 95% UD)	Present at cull site * Geodesic distance to cull sites (sum) * Connection strength to removed bird (max)	Predictor	Fixed	Mixed
	Moult site in cull year	-	Random	Categorical

Changes in the strength of association amongst birds following the cull were analysed in two ways. The first operated at the population level and quantified the extent to which association patterns were maintained post-cull. The second assessed the relative importance of treatment, social proximity and

geographic proximity in predicting the extent to which individual birds retained their previous associates.

In the first analysis, MRQAP (multiple regression quadratic assignment procedure (Dekker et al. 2007)) was used to compare two matrices of HWI association strengths: one calculated from pre-cull resightings (July 2012-June 2013), the second from post-cull resightings (July 2013-June 2014). MRQAP allows association matrices (matrices giving the number of times individual *i* has been seen with individual *j*, indexed using HWI) from different periods to be compared to understand how well one informs the other. MRQAP was run in R (version 3.2.0, package asnipe (Farine and Whitehead 2015)).

In order to tease apart how treatment (presence at a cull site), strength of social connections to removed birds and spatial proximity to a cull predict the retention of pre-cull associates following the cull, a linear mixed model containing these predictors was constructed (Table 6.5). It was predicted that being present at a cull site, losing strong associates or moulting very close to a cull site would perturb the social network, meaning that birds experiencing these conditions would retain fewer of their surviving connections and at a lower rate than birds that were not present at cull sites. The change in association strength before and after the cull was calculated by subtracting the association strength in the post-cull year from the association strength in the pre-cull year for each dyad. Since the direction of this change was an artefact of the calculation process, these values were given as absolutes. The linear mixed model was run in R (version 3.2.1, package 'lme4' (Bates et al. 2015)), with the additional use of package 'lmerTest' (SAS Institute 1978; Schaalje et al. 2002) .

Table 6.5. Terms used in permutation models of association strength pre- and post-cull.

Terms	Type		
Presence at cull site	Predictor	Fixed	Categorical
Connection strength to removed bird (max)	Predictor	Fixed	Continuous
Sum geodesic distance to all cull sites	Predictor	Fixed	Continuous
Connection strength to removed bird (max) * Sum geodesic distance to all cull sites	Predictor	Fixed	Interaction
Collar ID nested within Moult site 2013	-	Random	Categorical

Ethics statement

Birds were removed as part of a planned management programme, under licence from Natural England. All removals took place screened from sight of the public and of the penned birds. Only adult birds without juveniles were removed; sites at which goslings were present were designated non-cull sites.

All work was carried out in the UK in accordance with University of Exeter and Animal and Plant Health Agency ethics guidelines, under Natural England and British Trust for Ornithology licences and with the land owners' permission. All field procedures were approved by the University of Exeter Ethics and Health and Safety Committees.

6.4 Results

Initial network conditions

Prior to the cull all social network metrics showed strong seasonal variation (Table 6.6). Modularity was highest, and clusters most distinct and discrete, during the breeding season with the frequent detection of strongly associating breeding pairs. The high frequency of pairs was reflected in the low mean degree and cluster size during the breeding season. The post-moult and winter periods are characterised by increased movement and social fluidity, with fewer, less distinct and larger clusters. During the moult, the movement of birds is constrained, leading to high modularity; however, they typically moult in large flocks, leading to high mean cluster size and degree.

Post-cull network characteristics

The cull removed half of the adult individuals from cull sites (50-66% across the three sites) and 20% of individuals within the moult network. Collared and ringed (n=16), ringed (n=2) and unmarked (n=21) birds were removed.

Observing perturbation at the population level

Following the cull, the goose social network split into a higher number of clusters and modularity was reduced (Table 6.6). Hence, marked birds did not associate together as frequently as before the cull; associations within social groups were weaker and social groups were not as distinct within the network (Figure 6.3).

The seasonal patterns observed post-cull followed those observed pre-cull but modularity was lower and social groups less distinct in all seasons other than winter. Although modularity declined between the moult and the post-moult period in both years, this effect was greater in the post-cull year (Table 6.6).

Table 6.6. Network-level metrics pre- and post-cull.

Network		Modularity	Mean cluster size (N clusters)	Path length (Δ)	Average degree (Δ)
Pre-cull	Moult (July 2012)	0.653	30.600 (5)	1.752	43.33
	Post-moult (Aug-Oct 2012)	0.494	15.625 (8)	2.029	26.05
	Winter (Nov-Feb 2012/13)	0.438	20.286 (7)	1.633	58.01
	Breeding (Mar-May 2013)	0.839	1.933 (30)	1.196	1.55
	Moult (June 2013)	0.695	7.143 (14)	1.240	17.42
Culls (3rd and 4th July 2013)					
Post-cull	Moult (July 2013)	0.558	10.250 (12)	1.875 (+0.123)	29.80 (-13.53)
	Post-moult (Aug-Oct 2013)	0.240	10.786 (14)	1.687 (-0.342)	60.66 (+34.61)
	Winter (Nov-Feb 2013/14)	0.613	5.160 (25)	3.410 (+1.777)	13.91 (-44.01)
	Breeding (Mar-May 2014)	0.720	3.652 (23)	2.452 (+1.256)	6.21 (+4.66)
	Moult (Jun-Jul 2014)	0.551	6.083 (12)	1.488 (+0.248)	14.49 (-2.93)
Whole-year pre-cull (2012-13)		0.443	30.600 (5)	1.499	80.484 (SD 23.895)
Whole-year post-cull (2013-14)		0.328	11.357 (14)	1.632	65.918 (SD 34.073)

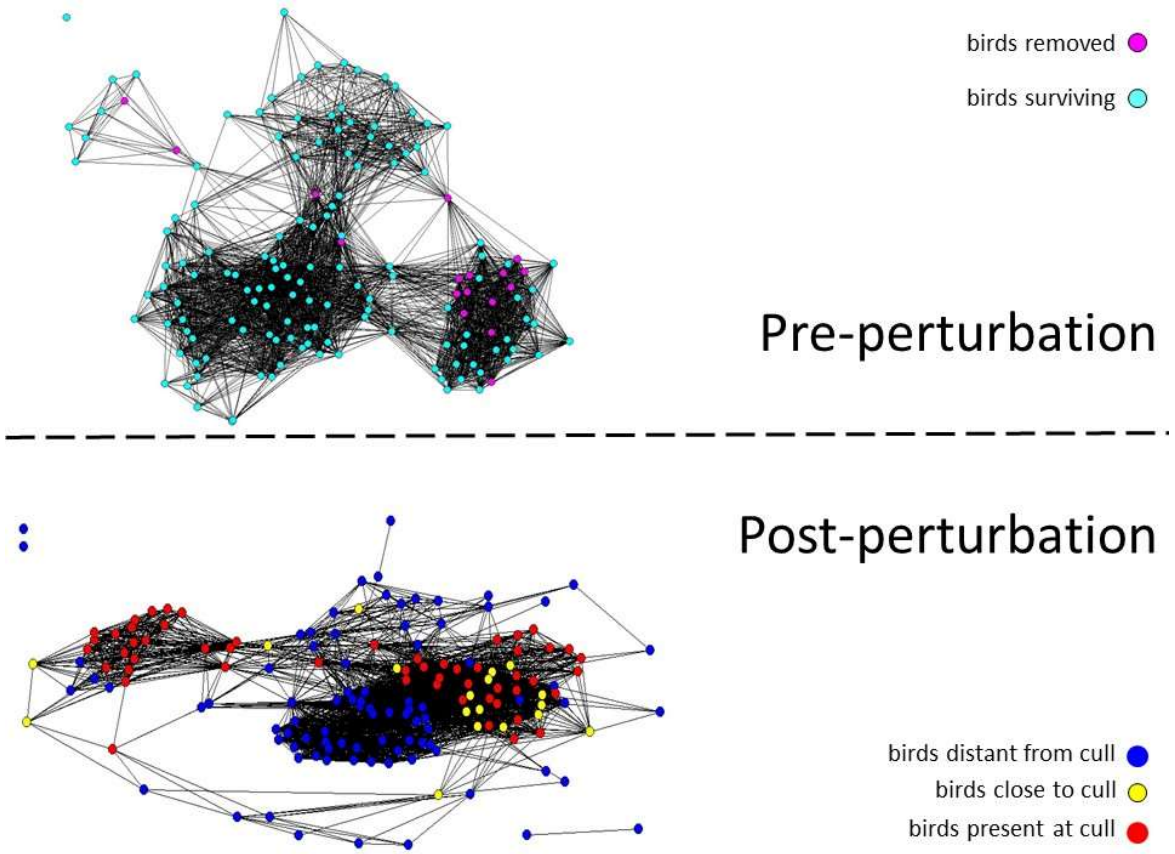


Figure 6.3. The social network pre- and post-cull. Each node is an individual bird and the edges between them indicate that they have associated within the time period given. For display purposes, edges are unweighted.

After the cull, the number of clusters in the goose network increased and their mean size decreased, reflecting a trend for marked birds to associate with fewer other marked birds. This dispersal of marked birds into different social groups is reflected in the longer path lengths seen in the network following the cull, particularly during the winter, breeding and moult periods. In the immediate post-cull period (post-moult 2013), the sharp drops in modularity and path length and rise in average degree suggest disruption in social structure arising from marked birds moving between social groups. These changes were seen both in comparison to the same season in the previous year and other seasons in the same year. Whole-year degree was lower and more variable following the cull (pre-cull $F_{1, 310}=8.75$, $p<0.01$).

At a global network level, preferential associations were observed to occur less frequently following the cull. The pre- and post-cull networks were permuted to assess the context of changes in modularity. When permutations were unrestricted, and sampling included all existing (though not all possible) connections, the modularity scores seen in both permuted networks were much lower than those seen in either observed network (Figure 6.4). However, restricting permutations to only intra-cluster connections led to modularity scores that were much higher than those seen in the real networks. All permuted networks showed modularity values that varied from the observed networks both pre- and post-cull. The network seen pre-cull is better represented by permutations of only existing intra-cluster connections, whilst post-cull modularity is closer to that achieved by unrestricted permutations, demonstrating a decrease in preferential associations.

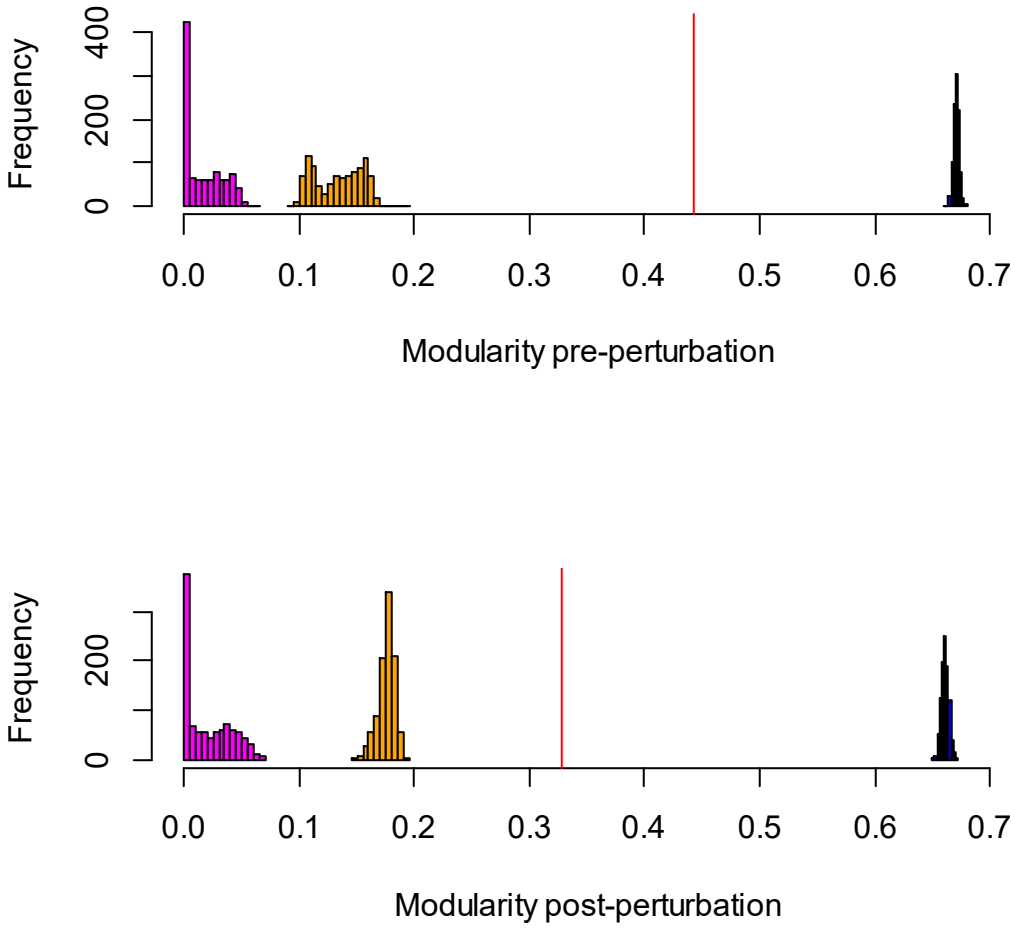


Figure 6.4. Modularity scores pre- and post-cull. In each case, the first distribution on the left is calculated by permuting all edges within the dataset without reference to known clusters, the second by permuting all realised edges (i.e. non-zero edges) and the distribution on the right is calculated by permuting only intra-cluster edges. The red vertical line indicates the modularity value calculated from the observed network.

Cluster persistence

When measuring the extent to which individuals changed social group following the cull, all clusters in the pre-cull network were observed to fracture (Figure 6.5). A bipartite graph showing changes in birds' social affiliations through time displays that whilst most of the members of each pre-cull social group remained together post-cull, several individuals switched social groups.

Thus, the core of each pre-cull social group formed the nuclei around which other birds, fragmented from other social groups, aggregated. Most birds maintained their social groups post-cull, with a minority of birds completely changing their social groups.

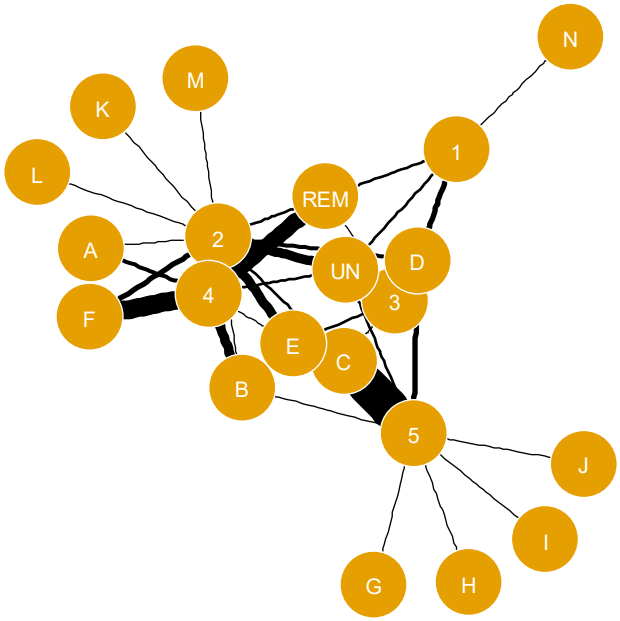


Figure 6.5. Network showing dissolution of clusters post-cull. Pre-cull clusters are numbered 1-5; post-cull clusters are labelled with the letters A-N. Birds that were not observed following the cull were placed in the UN cluster and birds that were removed were placed in a single cluster ('REM'). E.g. birds from pre-cull cluster 1 moved into post-cull clusters D and N, the 'removed' category and the 'unknown' category.

The individual-level linear mixed models predicting fragmentation triggers bears this out: clusters were resilient to the removal of individuals. All birds maintained their associations with a higher proportion of their surviving associates if they lost a large proportion of their social cluster in the cull (Figure 6.6), but this was more pronounced for birds that moulted at a cull site.

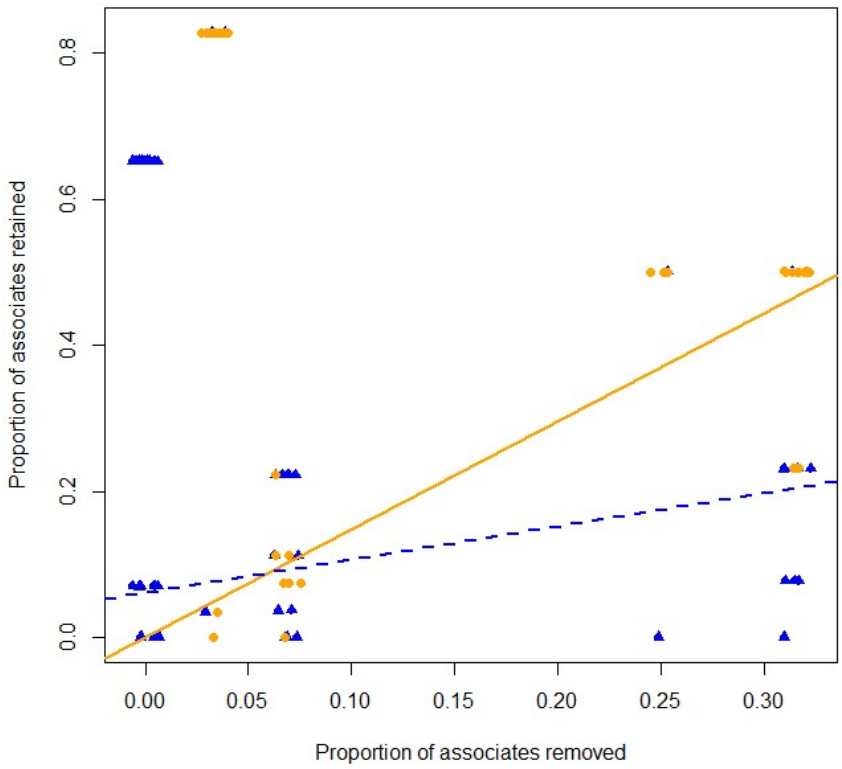


Figure 6.6. The correlation between losing pre-cull associates in the cull and maintaining relationships with surviving associates from the same social group. Data from birds that moulted at a cull site are shown in orange (solid lines, circular points), data from birds that did not moult at a cull site in blue (dashed lines, triangular points). For graphical purposes only, jitter (a small amount of random noise) has been applied to data points and lines are taken from linear models that account for social cluster size.

Model averaging of a candidate model set by AIC identified two key predictors of birds retaining their associates: the proportion of previous associates removed in the cull and the size of the bird's social cluster following the cull (Table 6.7), a crude measure of gregariousness post-cull. Spatial proximity to a cull site did not appear in the top model set, suggesting that it was not predictive of whether birds maintained their relationships with surviving members of their cluster.

Table 6.7. Conditional model estimates for terms in models explaining variance in the proportion of pre-cull associates retained post-cull (terms within models <4 ΔAIC of top model).

Terms	Estimate	SE	Adjusted SE	z value	p
(Intercept)	0	0	0	NA	NA
Number of birds in post-cull cluster	0.944	0.231	0.234	4.041	<0.001
Proportion of new associates in post-cull cluster	-0.817	0.054	0.055	14.952	<0.001
Proportion of associates removed in the cull	-0.003	0.272	0.275	0.011	0.991
Present at a cull site	0.154	0.175	0.175	0.882	0.377
Present at a cull site* Proportion of new associates in post-cull cluster	**-0.221**	**0.0822**	**0.083**	**2.656**	**0.008**
Present at a cull site* Proportion of associates removed in the cull	**0.180**	**0.079**	**0.079**	**2.262**	**0.024**

Movement of birds

Most birds were observed to have larger home ranges in the year post-cull than the year pre-cull (mean range pre-cull= 27.30km^2, mean range post-cull=45.77km^2, exact binomial test=0.670, 95% CI=0.572-0.758, p<0.001). However, whether or not a bird increased its range size was not correlated with proximity to the cull: a generalised linear model with binomial fit found that birds that were i) present at a cull site, ii) closely associated with birds that were removed in the cull or iii) moulted at a site contiguous with a cull site were no more likely to increase their range than birds that were more distant to the cull (Chi^2_5=3.1347, p>0.1, Table 6.8).

Table 6.8. Coefficients of binomial model of increased range and the effects of spatial and social proximity to the culls.

Terms	Estimate	SE	z value	p
(Intercept)	0.8128	0.9474	0.858	0.391
Moulted at a site contiguous with a cull site (spatial/treatment)	-2.2310	2.0447	-1.091	0.275
Moulted at a cull site (spatial/treatment)	-0.4231	1.9873	-0.213	0.831
Connection strength to removed bird (social)	-0.1189	2.1476	-0.055	0.956
Moulted at a site contiguous with a cull site * Connection strength to removed bird	1.1325	4.0190	0.282	0.778
Moulted at a cull site * Connection strength to removed bird	1.2192	3.4833	0.350	0.726

Amongst those birds that did increase their range following the cull, their proximity to the cull, in both geographic and social space, was strongly and significantly negatively correlated with the distance they moved ($Chi^2_7=24.745$, $p<0.001$, Table 6.9a). Birds that were present at a cull site, closely connected to birds that were removed or moulted close to cull sites had smaller post-cull home ranges than those birds at greater social and spatial distance from the cull (Figure 6.7a).

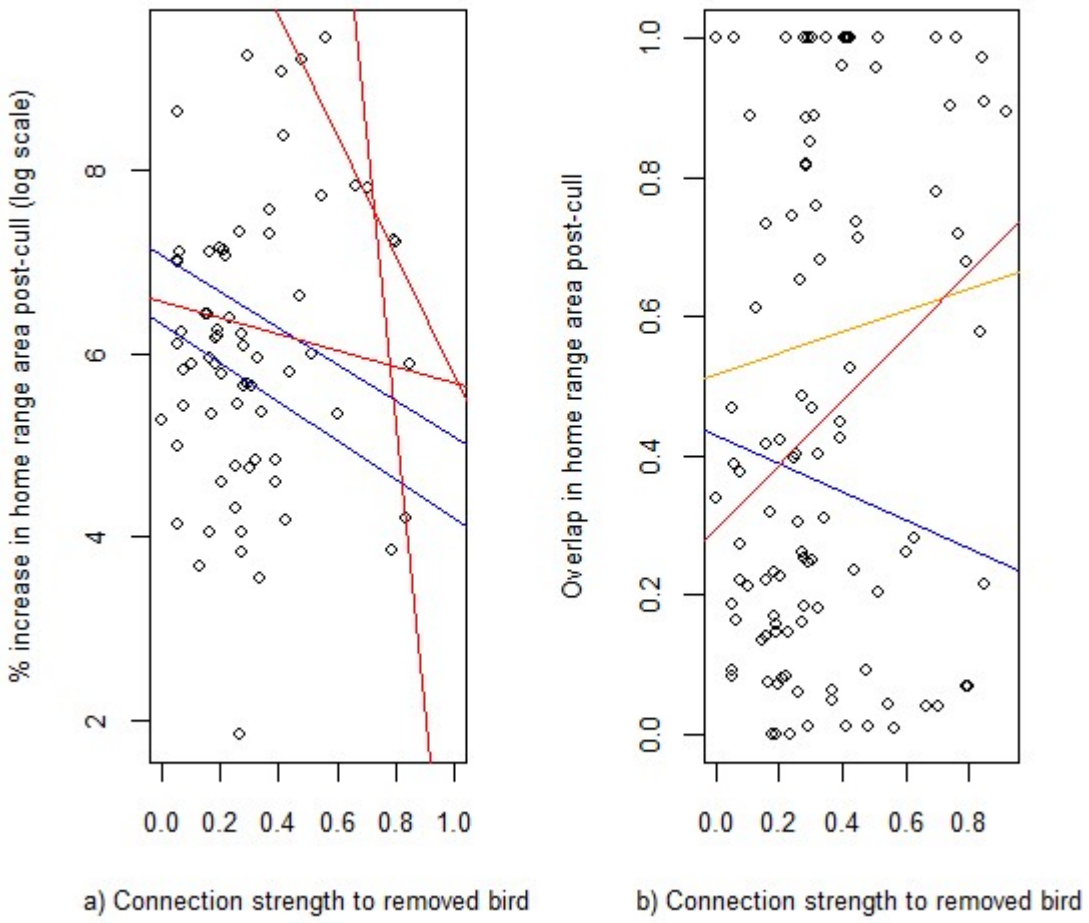


Figure 6.7. The change in a) home range and b) home range overlap shown by birds following the cull as a function of their maximum connection strength to a removed bird. Lines are taken from linear models of birds that moulted at non-cull sites (blue), cull sites (red) and near-cull sites (orange, overlap plot only).

Proximity to the cull was also important in predicting the overlap shown in ranges pre- and post-cull (Figure 6.7b). Birds present at cull sites showed higher overlap of ranges between years (Chi^2_6=13.115, p=0.0412, Table 6.9b).

Table 6.9a. Model coefficients for those birds that increased their range following the culls (n=69) and the variation explained by spatial and social proximity to culling. Significant interaction term is shown in bold.

Terms	Estimate	SE	DF	t value	p
(Intercept)	74.285	28.093	4.099	2.644	0.056
Presence at cull site	-134.778	37.538	9.103	-3.590	0.006
Geodesic distance to cull sites (sum)	-3.624	1.434	4.169	-2.528	0.062
Connection strength to removed bird (max)	-91.015	34.556	4.002	-2.634	0.058
Sex	-0.145	0.361	27.409	-0.402	0.691
Presence at cull site * Geodesic distance to cull sites (sum)	7.412	2.038	11.073	3.637	0.004
Presence at cull site * Connection strength to removed bird (max)	178.192	46.386	8.283	3.841	0.005
Geodesic distance to cull sites (sum) * Connection strength to removed bird (max)	4.665	1.777	4.098	2.625	0.057
Presence at cull site * Geodesic distance to cull sites (sum) * Connection strength to removed bird (max)	**-9.554**	**2.520**	**10.364**	**-3.791**	**0.003**

Table 6.9b. Model coefficients for model of range overlap post-cull and the variation explained by spatial and social proximity to the culls. Significant interaction term is shown in bold.

Terms	Estimate	SE	DF	t value	p
(Intercept)	-0.800	0.610	22.95	-1.313	0.202
Presence at a cull site	1.595	0.946	21.89	1.687	0.106
Geodesic distance to cull sites (sum)	0.073	0.029	28.82	2.492	0.019
Connection strength to removed bird (max)	2.610	1.028	51.49	2.538	0.014
Presence at a cull site * Geodesic distance to cull sites (sum)	-0.094	0.042	25.18	-2.259	0.033
Presence at a cull site * Connection strength to removed bird (max)	-3.283	1.565	70.51	-2.099	0.039
Geodesic distance to cull sites (sum) * Connection strength to removed bird (max)	-0.119	0.046	43.30	-2.625	0.012
Presence at a cull site * Geodesic distance to cull sites (sum) * Connection strength to removed bird (max)	**0.161**	**0.063**	**65.42**	**2.557**	**0.013**

Table 6.9c. Model coefficients for model of site use (movement propensity) post-cull and the variation explained by spatial and social proximity to the culls. Significant predictor terms are shown in bold.

Terms	Estimate	SE	DF	t value	p
(Intercept)	-1.169	1.697	20.27	-0.689	0.499
Presence at a cull site	2.890	2.053	81.03	1.408	0.163
Geodesic distance to cull sites (sum)	0.004	0.077	54.01	0.049	0.961
Connection strength to removed bird (max)	**3.931**	**1.648**	**75.87**	**2.385**	**0.020**
Geodesic distance to cull sites (sum) * Presence at a cull site	**-0.199**	**0.089**	**77.99**	**-2.232**	**0.029**

Social distance, the connection strength between each bird and the culled bird to which it was most strongly connected, was the strongest predictor of small-scale movement. There was a strong, significant positive correlation between the association strength to a culled bird and the number of sites used post-cull (Table 6.9c). This meant that, for birds that were not themselves present at a cull, losing a close associate resulted in them using a mean of one extra site, whilst losing a weak associate resulted in them using a mean of one fewer site (in comparison to the bird's previous year's movement). Cull-site birds tended to use fewer sites than non-cull-site birds in the year post-cull (Figure 6.8).

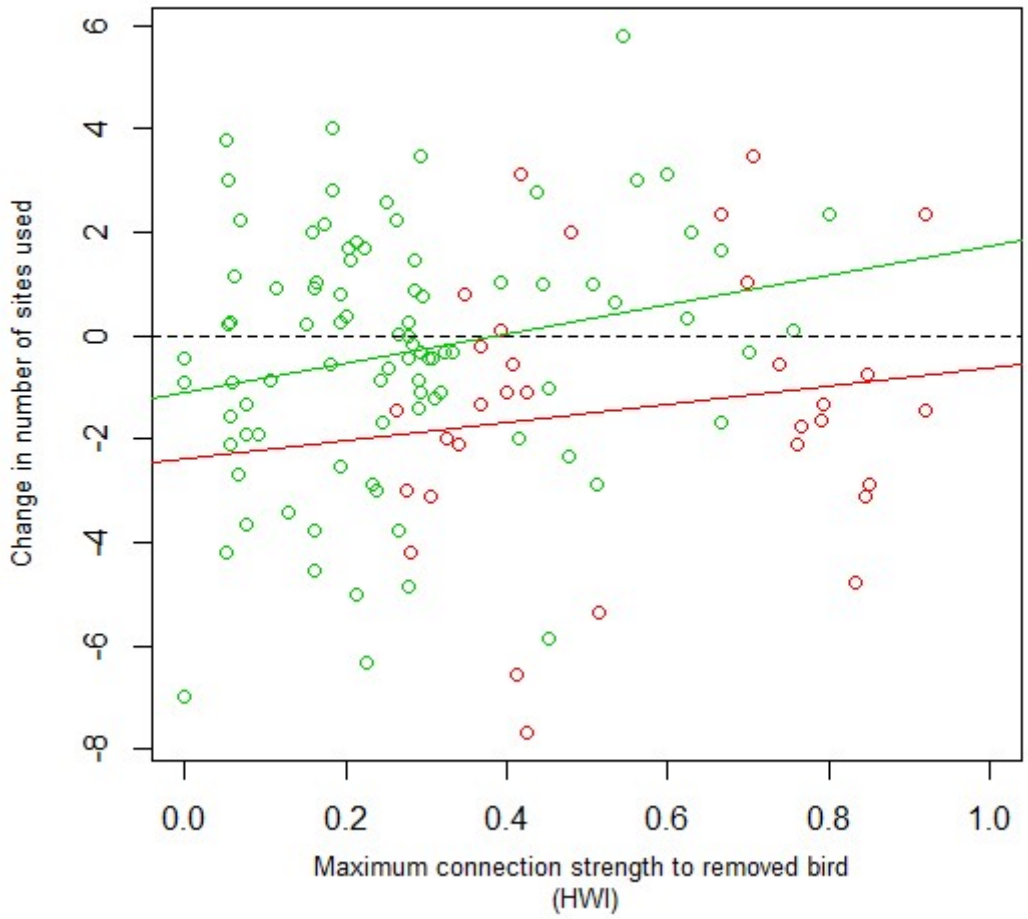


Figure 6.8. Change in number of sites used between pre-cull and post-cull years for birds moulting at cull sites (red) and non-cull sites (green) as a function of connection strength to closest culled associate. Lines are taken from linear models. Dashed line indicates no change in the number of sites used.

Persistence of preferential associations

Correlational analysis using MRQAP found a strong, significant correlation between association strengths shown by all birds to their associates between years ($F_{1, 7258}$=2416, p<0.001). In all, ~25% of variation in the post-cull matrix was explained by the pre-cull matrix (i.e. the pre-existing social structure, adjusted r^2=0.2497). This indicates that birds were maintaining many of their

previous associations at a similar level within the population following the cull (Figure 6.9).

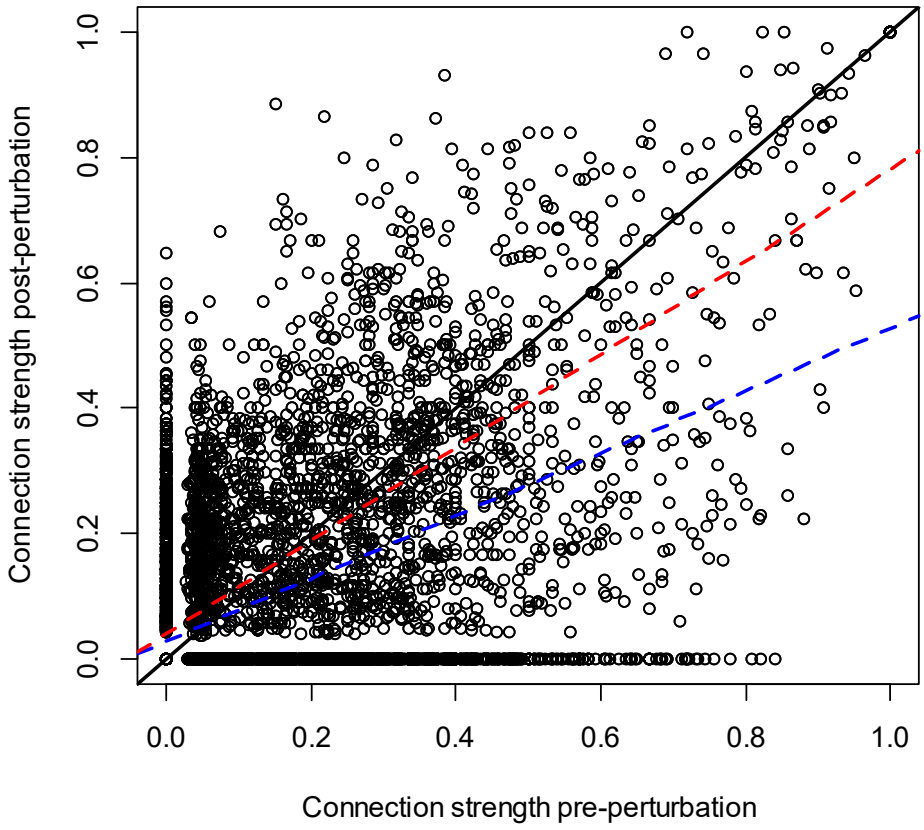


Figure 6.9. Repeatability in association strength pre- and post-cull. The solid line indicates 1:1 association strength, whilst the dashed lines are taken from linear models of association strength pre-/post-cull for cull-site (red) and non-cull-site (blue) birds.

Treatment and social and geographic proximity to the cull were found to predict the pre- to post-cull change in association strength between dyads (permutation test, $p<0.001$) in additive fashion (Figure 6.10). Birds that were present at the cull associated more strongly following the cull. In addition to this, birds that were close to the cull in social and geographic terms showed increases in their connection strength to previous associates following the cull (Table 6.10). It appears that associates are important to all birds with

perturbed networks, but particularly so if they also had close associates removed.

Table 6.10. Fixed effects of model looking at the change in association strength between each dyad between years.

Terms	Estimate	SE	DF	t value	p value
(Intercept)	0.180	0.052	87	3.439	<0.001
Presence at cull site	**0.050**	**0.014**	**87**	**3.654**	**<0.001**
Connection strength to removed bird (max)	-0.254	0.104	87	-2.453	0.0162
Sum geodesic distance to all cull sites	-0.009	0.003	87	-3.425	<0.001
Connection strength to removed bird (max) * Sum geodesic distance to all cull sites	**0.009**	**0.004**	**87**	**2.190**	**0.0312**

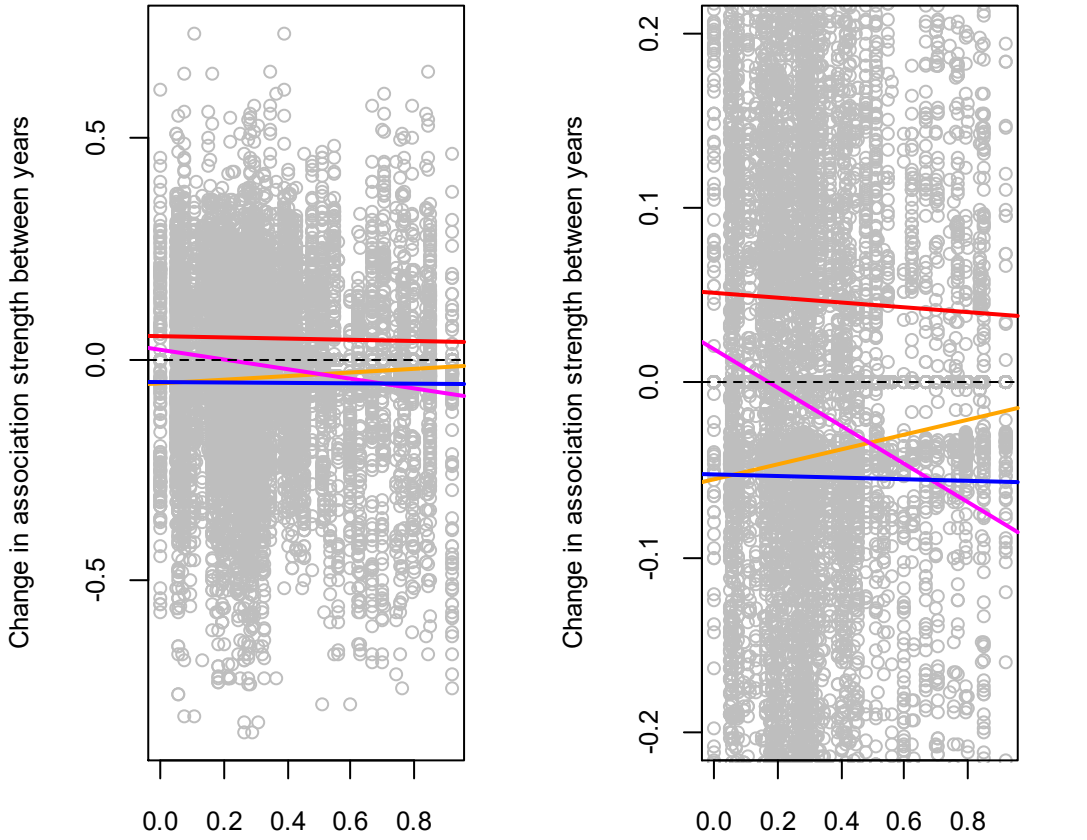


Figure 6.10. The relationship between social distance (connection strength to removed bird), treatment (presence at cull site) and geographic distance (distance to all three cull sites) and its correlation with the change in association strength following the cull. a) shows the full range of the data, b) focuses on changes -0.2-0.2 connection strength (HWI). Lines are taken from linear models of cull-site birds (red=moulted close to all cull sites, orange=moulted distant to one or more cull sites) and non-cull-site birds (pink=moulted close to all cull sites, blue=moulted distant to one or more cull sites).

6.5 Discussion

The structure of the network itself changes considerably following the cull, with clusters of marked birds fragmenting and resulting in many more social clusters, each containing fewer marked birds, with little contact between clusters of previously associating marked birds in the year post-cull. In the immediate post-cull period, the level of network structure was much lower than in the same post-moult period in the previous (non-cull year), leading to a network in which birds contacted more associates, apparently without the same level of social preference as seen in other seasons. Contrary to expectations, birds ranged less far and explored less new territory following the cull if they lost close associates. This contraction of home range and use of familiar sites is borne out in analysis of the social network structure. Pre-cull connections became stronger following the cull, and cull-site birds retained a higher proportion of their previous associates than control-site birds. These are the first analyses using social networks to reveal changes in bird social behaviour in the wild following a cull and support pre-emptive, rather than reactive, culling.

The pre-cull social network was strongly seasonal but nevertheless remained consistently highly structured into distinct clusters. As predicted, the cull appeared to be followed by a short period of 30-60 days of high social fluidity, with all birds connected in a homogeneous network that would facilitate the swift transmission of information or disease. This supports previous studies in badgers that found ranges (and potentially contact rates) to increase post-cull (Riordan et al. 2011). Following this post-moult period, the social network became more structured; typically the pre-cull clusters had fragmented and the occupants had formed several small clusters, among which there was little contact. This follows what was seen in an experimental perturbation of captive Atlantic mollies (*Poecilia mexicana*), in which perturbation (remixing the population into new social groups) was immediately followed by a period with increased mixing and reduced social hierarchy before re-establishment of the status quo (Bierbach et al. 2014). This increase in clustering, which resulted in longer path lengths across the network, would theoretically lead to relatively

slow transmission rates of infectious disease or information across the network.

Canada geese social networks appear to be resilient to the removal of individuals in the medium-long term, with cull-site birds strengthening their connections to their previous associates post-cull, meaning that social clusters may become smaller but their core composition is unchanged. This may be due to a selective advantage to retaining and maintaining connections in unpredictable environments rather than forming new associations (Mallpress et al. 2015). Canada goose populations have expanded throughout the UK since the first introductions in the 1800s (Allan and Feare 1994) and harvest-induced mortality, which exerts strong selection pressure (Allendorf and Hard 2009), may have contributed towards selecting for adaptability in this species. This was also supported by our results on the fracturing patterns shown by clusters. Birds were seldom found to move between clusters alone but instead moved with one to six associates, suggesting that geese face little cost moving between flocks provided that they retain a small number of close connections. This tallies with previous research suggesting that dominance hierarchies are determined by the number of the individual's close associates (Poisbleau et al. 2006). It also suggests that it is the individual's immediate social environment, rather than its broader social group, that has the strongest influence on its behaviour. It would then follow that the removal of very close associates is likely to elicit change in an individual's social position or behaviour.

Interestingly, connection strength to culled birds was found to be strongly predictive of number of sites used post-cull, with birds that lost close associates using more sites post-cull. This measure, capturing movement between sites that are typically geographically close, is reminiscent of birds moving in response to social factors (displacement by aggression or competition) or disturbance (Bijleveld et al. 2012). It appears that even small changes to a bird's social network such as losing a single strong associate results in birds moving more often (though not necessarily alone). This high movement between proximate sites may be costly in terms of the time

available to graze or rest since the individual must spend time at each site assessing risks and familiarising itself with the terrain, This provides further support that the cost of abandoning social ties following perturbation outweighs the potential benefit of switching social groups to distance oneself from the cull.

Contrary to expectations, birds that moulted at cull sites did not range more widely in the year following the cull than birds that moulted at non-cull sites. Previous research in badgers has suggested that individuals in areas where culling took place ranged further following the cull (Riordan et al. 2011). The response shown here by birds from cull sites to increase their home range area but to do so much more modestly than control-site birds and to do so with greater overlap of their previous home range suggests a behavioural response to the cull. Several taxa have been noted to reduce their movement levels (Lima and Dill 1990; Johansson and Andersson 2009; Rodgers et al. 2011) under high risk of predation. Reducing movement may reduce the likelihood of encountering a predator or allow the diversion of resources into the production of defensive structures. Voles (*Microtus spp*.) were reported to show intermediate movement levels under high predation risk (Banks et al. 2000): a trade-off between low movement levels that reduce the likelihood of encountering a predator and high movement levels that disguise the prey's likely location. The range contraction seen in this species may be representative of a wider phenomenon in prey species for decreased movement as a response to high predation.

Culling did lead to global changes in the network and changes in birds' behaviour; however, the implications of perturbation for higher processes, such as disease transmission, are likely to be nuanced. The specific infectious agent and the timing of the outbreak will determine whether the perturbation seen in this system facilitates disease transmission (Prentice et al. 2014) or limits it. Most birds' behaviour shifted to them maintaining a smaller number of connections more strongly and ranging less widely, thus becoming less likely to transmit infection widely. Also, path lengths increased following the cull, meaning that outbreaks may be smaller or confined to parts of the network. If

culling were to be undertaken for disease control purposes then these findings suggest that doing so in the summer in anticipation of a winter outbreak would be beneficial, since the reduction in mixing seen in the post-cull winter network, and the lower ranging behaviour shown by cull-site survivors, are both likely to reduce contact rates. However, the increased mixing seen in the post-moult period suggests that culling an infected population during this period is likely to increase contact rates and spread disease more widely throughout the population.

Social perturbation is not only manifested in changes in movement behaviour and contact rates. Social challenges and dominance may carry costs via the increased production of glucocorticoid stress hormones (Sands and Creel 2004). The analyses of movement propensity suggest that individual Canada geese that lost close associates were more likely to show increased small-scale movement: 'hops' between lakes that could be the result of avoiding social challenges. If an individual does lose dominance following the cull, there may be short- and long-term consequences for its stress hormone levels. Given the importance of cortisol and stress hormones on the immune system in many species (Maule et al. 1989; Kunz-Ebrecht et al. 2003; Segerstrom and Miller 2004; Dosmann et al. 2015), it will be important in the future to establish the impact of culling on social species' stress responses and resistance to infection.

Culling of wildlife is often a controversial topic, both in terms of its ethics and its efficacy. Culling for disease control can only be justified where evidence supports that culling will indeed reduce disease incidence. Reducing the number of diseased hosts may be important; however, the crucial reduction required is in the number of contacts between infected and naïve hosts, and naïve hosts' contact with pathogens within the environment. Where culling disrupts the social structure, the reduction in the number of infected hosts must be greater than any rise in contact rates if disease is to be contained. The evidence in this population suggests that culled flocks of Canada geese show a period of increased mixing followed by a reduction in movement levels and the maintenance of social ties in the year following the cull. The timing is

confounded by goose seasonal behaviour, given the necessity to cull in the moult, which is followed by increased mixing. However, this does not change the central fact that culling an infected population has the potential to increase the spread of disease to more social groups. In contrast, culling a Canada goose population in advance of infection may result in smaller ranges and social groups that constrain future disease spread.

In conclusion, in the months immediately following the cull, a period of network disruption was observed that may equate to wider roaming and is likely to reflect an increase in associations between previously unconnected birds. In the year following the cull, birds that were present at cull sites appear to show entrenched social and movement behaviour. Cull-site survivors maintained their previous associations at a higher rate than control birds, whilst birds from non-cull sites ranged further and increased their use of novel sites. The management implications of this work depend on the infection status of the population at the moment of perturbation: culling uninfected populations in anticipation of a future outbreak is likely to reduce disease transmission, whilst culling an infected population may increase contact and transmission rates.

7. General discussion

Overview

This thesis described the social structure and movement behaviour of the free-living Canada goose before and after a partial cull of the population. These studies reveal the impact of culling on goose social structure and the potential impact of culling on disease transmission dynamics. This thesis suggests that, geese have a highly structured social system, with transient flocks formed of smaller, more stable groups. There is strong seasonal variation in movement levels, with birds ranging furthest in autumn and using the highest number of sites in winter. Birds appear to end the year in similar condition to their social group. Whilst social affiliations strengthen following culling, there is a period of social network disruption following the cull that exceeds the level seen in a non-cull year. Culling may increase the transmission of disease during this post-moult period but in the long term cull survivors showed entrenched social and movement behaviour, strengthening their connections to their surviving associates and moving less far in the year following the cull.

Goose social structure

Social networks reveal the strong structure present in the goose social system. Even in winter, when geese can be observed roosting and grazing in flocks of several hundred, apparently unchanged for weeks on end, the pattern of associations reveals social affiliations. Networks complement our knowledge of *Branta* natural history, demonstrating both the segregation expected during the breeding season and the limited mobility during the moult (chapter five). Biological relationships, such as the preferential associations seen between breeding pairs, can be divined from social networks at an earlier stage than they would be confirmed in the field (chapter four). As in other social systems, the goose social system appears to be fractal, with

groups increasing in size by a factor of approximately three with every increase in the social circle (Hill et al. 2008) (chapter four).

The study population at the Cotswold water park appears to include three separate subpopulations with ranges centred around three broad locations: the eastern population, centred around Lechlade; the western population, centred on Cerney Wick and a social group that was only observed at one of the southern-most lakes, lake 57. Birds from both the eastern and western populations were observed at a site roughly equidistant between the populations, lake 200, but few birds made the move from one side of the water park to the other. The three subpopulations were further divided in the social network by a community detection algorithm (the walktrap algorithm (Pons and Latapy 2005), chapters four and six) into five social groups. Birds were generally consistent in their use of sites and showed fidelity to breeding and moult sites between years (chapter three). Birds had a mean of 80 associates (in the year pre-cull).

What structures the social network in the Cotswold population? Beyond geography, with region being a likely structuring force, breeding status appears to structure the social network. The importance of the family is well known in *Branta* and *Anser* species, with family connections influencing dominance position and affiliative behaviour (Fox et al. 2002; Poisbleau et al. 2006; Poisbleau et al. 2008; Poisbleau et al. 2010). The social bond between breeding pairs was visible in winter networks (chapter four) and visible in birds' positioning in the field (chapter four). Birds that bred successfully were observed to have fewer associates but stronger connections to those associates (chapter three).

Heterogeneity in the networks

We know that some individuals will be more important in the transmission of disease than others (Lloyd-Smith et al. 2005), just as 50% of the population must be at or above average. Individuals that have lots of associates,

associate with several social groups or travel great distances have the potential to transmit infection more widely than less gregarious or mobile conspecifics (Small et al. 2006). The key is whether i) 'superspreader' attributes are correlated, so that individuals with large social circles also bridge otherwise separate social groups and range further; or ii) whether superspreaders can be identified by age, class or characteristic. Superspreaders differ from super-excretors (Smith et al. 1995) or asymptomatic carriers (Newman et al. 2009; Dhondt et al. 2012) in that their potential importance in disease transmission arises from their social and movement behaviour rather than their innate immune capabilities. Chapter three found evidence of potential 'superspreaders': those birds with the potential to spread disease far and wide in both the social network and in the landscape. In Canada geese, individuals that had the highest numbers of associates also contacted birds from a larger number of social groups. These individuals also moved a lot further in some regions of the study area and very slightly less in others. However, strength of connection correlated negatively with home range area and number of sites used. This suggests that the role of highly mobile, highly gregarious birds is correlated with the infectiousness of the agent and its stability within the environment. For diseases that are thought to require closer or repeated exposure, such as tuberculosis, the role of these flighty birds should not be overstated, whilst for easily transmissible pathogens that can remain infective within the environment (Brown et al. 2009) they could potentially be superspreaders.

Linked to this, all social groups are not equal in the transmission of disease (chapter four). The five social groups identified in the pre-cull Cotswold population showed very different levels of movement and body condition. Poor body condition is likely to be a contributing factor in whether an individual contracts disease and the severity of infection (Kortet et al. 2003). The differences seen between social groups in their movement patterns and relative body condition provides another layer of information that may inform disease transmission and progression in this system.

Seasonality

Whilst the seasonality in contact rates seen in the Cotswold geese in chapter five chimes perfectly with what is known about their natural history, it is likely to be the mirror image to that seen in many other species. Many species breed colonially and thus contact rates in species such as albatross (e.g. the black-browed albatross, *Thalassarche melanophris* (Wakefield et al. 2014)) are likely to peak during the mating and breeding seasons. This would lead to a peak in contact rate just at the point when new, naive, vulnerable hosts enter the population. This vulnerability may be exacerbated by the necessity in certain systems (e.g. bats (Hayman et al. 2013; Langwig et al. 2015)) for young to huddle together. Disease transmission in these systems is likely to look very different to the goose system, in which contact rates are high in summer, autumn and winter, though path lengths are shortest (and transmission potentially fastest) in autumn. Geese, like many nesting birds, defend a territory whilst incubating and raising very young goslings, potentially reducing their chicks' exposure to infection by conspecifics during their most vulnerable stage. In cattle, calves have been observed to have distinctive social network connections to their mothers (Swain and Bishop-Hurley 2007) and in the bottlenose dolphin *(Tursiops spp.)* juveniles connections were weighted towards adults, particularly adult females (Stanton and Mann 2012). This indicates that juveniles in structured social systems do not mix with impunity.

The effect of season on the movement of a resident species that infrequently moves further than a few kilometres is possibly of niche interest. Epic migrations and arduous journeys between staging sites are captivating because of the physical reserves and the extraordinary navigation skills they require. However, when considering disease transmission, it can pay to think small. Whether an individual is exposed to an environmental pathogen depends on its use of the environment at an incredibly fine scale. Dabbling ducks' higher levels of avian influenza virus may partially be the result of their feeding in shallow water, where the virus is most prevalent (Munster et al. 2007). During the moult (in June and July), geese at the Cotswold water park

frequently roosted on the water, islands, and gravel embankments within lakes. During the remainder of the year they use the fields around lakes and, most frequently in winter, pasture not bordering waterbodies. These differences in site use predispose the geese to different companions. Canada geese were seen with greylag geese (*Anser anser)* most often at sites bordering water, whilst they were observed grazing near mute swans *(Cygnus olor)* mostly at pasture sites and on arable fields (which seldom bordered water). Canada geese seldom grazed with smaller species (e.g. mallards *(Anas platyrhynchos)*, moorhens *(Gallinula chloropus)* and coots *(Fulica atra)*, though they were seen close together on water, particularly on amenity lakes. Interspecies interactions are thus dependent on the habitat used and subject to seasonal variation in a similar fashion. Since pathogens' persistence in water and on fomites varies (Stallknecht et al. 1990; Brown et al. 2009), fine-scale patterns of site use may be important in predicting interspecific interactions and the potential for transmission (MacGregor et al. 2011).

Changes in social structure following culling

To the crux of this thesis: the changes in social structure observed following culling. The cull appeared to be immediately followed by disruption of the social network, with the network following the cull being less modular and more homogeneous than in the equivalent season in a non-cull year. Bonds strengthen and, when social groups dissolve, the majority of the group (or relatively large sections) remain together as a unit and either join or form a new social group. Social groups of marked birds were smaller following the cull, even accounting for the reduction in size as a result of the cull (chapter six). The changes in movement behaviour, with lower ranging behaviour following the cull, seen by cull survivors here contradict the movement behaviour seen following a cull in badger populations (Tuyttens et al. 2000). However, this was the long-term ranging behaviour and the network metrics from the post-cull period suggest a period of increased movement, which may explain the inconsistency. Interestingly, the emphasis on maintaining social bonds following the cull supports recent work which found that guppies

(Poecilia reticulata) under high predation pressure formed smaller groups that were both more stable and more strongly connected (Heathcote et al. 2017). Heathcote et al. also suggest that maintaining a strong social group naturally places a limitation on group size.

The Cotswold dataset gives a detailed picture on structural changes following the cull, but only compares two years (though control sites in the cull year allow some temporal effects to be set aside). Culling also took place in the Thames population, with culls during the moult of 2002, 2003, 2004 and 2005. It is interesting that, in the autumn following the 2002 cull (which followed a cull hiatus) and the autumn following the 2004 cull (which was twice the size of previous culls during the study period), the proportion of birds infected during the post-moult period appears to be higher than in other post-moult periods. The long-term Thames dataset gives a more general picture on population-level patterns, though with a lower proportion of marked individuals resighted more than once and more variable resighting effort. Despite the dataset's limitations, this rise in transmission may be analogous to the decline in modularity seen in the autumn following culling in the Cotswold population.

Management

These findings have the potential to inform the management of wild social birds. However, no one control strategy (beyond, perhaps, local annihilation of the species) will reduce the level of every pathogen. Taking the results of chapter three, it might be preferable to cull non-breeders (with their larger social circles including more social groups) for easily transmissible agents or agents that chiefly spread via fomites or the environment. Conversely, if looking to contain the transmission of agents requiring close contact or frequent exposure, and given the high likelihood of nearest neighbours in the field being close associates (chapter four), these results might suggest culling the social groups with the highest levels of breeding pairs and families. Similarly, the timing of the disease peak must inform the management strategy. Culling in summer is likely to heighten the autumn transmission peak

but may lead to a reduction in transmission activity following this initial peak. Therefore, culling during the summer moult can be advised *if the population is not already infected or infection is expected during the autumn.* Under other conditions (for example, an infection amplified by goslings or juveniles (Van Dijk et al. 2014)), culling during the summer moult reduces the number of potential hosts, may be followed by reduced formation of new associations and ranging distances, and thus could achieve its aim of reducing disease transmission. Finally, in cases where the disease (or possibly parasite) to be controlled disproportionately affects birds in poor condition, chapter four suggests that targeting and removing entire groups in poor condition rather than spreading effort across groups is advised. To allow this to be completed more rigorously without the need to catch and weigh geese, developing an abdominal profile index of condition for birds in the field, as exists for Brent geese *(Branta bernicla hrota)* (Silk 2014) and barnacle geese *(Branta leucopsis)* may be a useful development.

Conclusion

In conclusion, this thesis has followed a wild (free-living) population through a cull and out the other side, tracking changes in social structure and movement behaviour. Along the way, this has provided insights into the factors structuring the goose social system and the potential of UK-resident Canada geese to transmit disease at fine and landscape scales. This work underlines the importance of the breeding pair in structuring the goose social system. In predicting disease transmission at a fine scale, it suggests that not all individuals are equal: it is likely that non-breeding individuals are more important in the transmission of easily transmissible agents (e.g. avian influenza) than breeding birds. Culling appears to be followed by a period of social network disruption and, in the medium-long term, social affiliations between cull survivors strengthened more than those of birds that were not present at cull sites. This thesis demonstrates the utility of social network analysis in answering questions about the basic ecology of a species and its responses to human intervention.

8. References

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